Malcolm M. Furniss

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OLEORESIN PRODUCTION IN THE RESISTANCE OF PONDEROSA PINE TO BARK BEETLES

by

Robert Z. Callaham

Research Forester

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SUMMARY

The loss of trees due to killing by bark beetles has been recognized for a long time as an important drain on the pine resources of the world. Not all trees are killed by these parasites; some prove to be resistant. Only in a few cases have foresters developed the ability to recognize the susceptible individuals. If the cause of susceptibility were known, recognition of susceptible individuals might be facilitated.

Numerous observers have noted in the field that the success of attacks by some species of Dendroctonus and Ips seems to be correlated with the ability of the host to produce oleoresin. Accordingly, the hypothesis is presented that the ability of a tree to produce oleoresin is the first critical factor governing its resistance to bark-beetle attack.

Several investigations were carried out to determine whether resistant and susceptible ponderosa pine trees have different potentials for exudation of oleoresin in response to bark-beetle attack. Further investigations were made to determine the causes for variation in oleoresin production potential.

Ponderosa pines of different age and vigor classes and risk ratings were tapped to determine their ability to produce oleoresin. The results of this study indicated that there was a very great variability between trees in their ability to produce oleoresin in quantity. No significant differences were noted between tree classes in the amount of oleoresin produced. An analysis was made of the duration of flow from the same trees. The data indicated that the rate of flow diminished more rapidly from the third through the sixth day after tapping in trees classed as highly susceptible to the western pine beetle. These results suggest that oleoresin exudation from the most susceptible trees would cease sooner than it would from the more resistant trees. Nevertheless, there might be no significant difference in the total amount produced at least during the first eight days after tapping.

Ponderosa pines were tapped at various positions along the bole. The nature of positional variation in flow during the first 24 hours after wounding was determined. There were no differences in flow between the four cardinal aspects at any position. On the other hand, there was a highly significant reduction in oleoresin flow in the upper portions of the trees. The California five-spined engraver beetle commonly attacks in this region of reduced oleoresin exudation.

An analysis was made of the weight of the pitch tubes found on very young ponderosa pines. These trees were growing in a very dense stand which had been subjected to heavy attack by the mountain pine beetle. The data showed that the pitch tubes formed on resistant (living) trees were much larger than those formed on susceptible (dead) trees. This finding represents a quantitative verification of the common field observation that resisted attacks are characterized by very large pitch tubes. An additional analysis was made of the data from dead trees of different dominance classes. Trees in the intermediate and suppressed classes are thought to be attacked first in the development of an epidemic. The results of the analysis showed that the largest pitch tubes were produced on the dominant trees, and the smallest pitch tubes were produced on the suppressed individuals. The results of this investigation definitely indicate that the amount of oleoresin produced by a young tree influences its resistance to the mountain pine beetle.

The results of these three investigations show a correlation between the oleoresin production capacity of ponderosa pine trees and their susceptibility to

certain bark beetles. It should be stressed that such correlation does not imply causation. Studies now should be undertaken to determine the success of bark-beetle attacks when the insects are confronted directly with different oleoresin production potentials.

Many factors have been found to influence the amount of oleoresin exuded by a tree. Some of these factors which were considered in investigations of ponderosa pine in this study were the following: viscosity of the oleoresin, the size and capacity of the resin ducts through which the oleoresin flows, and the rate of radial growth.

Viscosity of the oleoresin was found to have a decided effect on the amount of exudate. This confirmed a similar finding for slash pine. More than twenty percent of the variation in the amount of exudation could be attributed to variation in viscosity. The more viscous oleoresin flowed more slowly. There was no indication of a change in the viscosity of the oleoresin exuding on successive days after wounding. The viscosity of the oleoresin did not differ from one side of the tree to another on the same tree. There was some indication of a change in viscosity in collections from different positions up and down the bole. The viscosity of the oleoresin did not appear to change from season to season. The temperature-viscosity relationship of ponderosa pine oleoresin was determined. Finally, variability in viscosity was shown to be almost completely determined by variation in the amount of turpentine contained in the oleoresin and by the composition of the turpentine. Turpentine composition was estimated from its specific gravity.

The number and the capacity of the transverse resin ducts could not be shown to influence significantly the flow of oleoresin from ponderosa pine. These facts were in contrast to the results reported by recent workers using slash pine. Both the number and the capacity of transverse ducts were found to vary significantly from one position to another on the bole. The number of ducts was lowest in the vicinity of mid-bole, and higher both at top and bottom of the bole. The capacity of the ducts steadily diminished from the base to the top of the tree. There was no indication of a change in number or capacity from one side of the tree to another at any level on the bole. The number of transverse resin ducts, but not their capacity, was found to increase with an increase in the radial rate of growth during the last ten years of growth.

The number of longitudinal resin ducts per tangential centimeter in the last twenty years of growth was significantly correlated with the yield of oleoresin during the first 24 hours after tapping. The number of longitudinal resin ducts per annual ring increased with ring width, but their density per unit area of transverse section decreased with increasing rate of growth. There was a significant correlation between the number of resin ducts in the longitudinal and transverse systems. The number of transverse ducts increased as the density of longitudinal ducts increased. The number of transverse ducts decreased as the number of longitudinal ducts per annual ring increased.

Variation in the annual rate of radial growth was not significantly associated with variation in the yield of oleoresin during the first 24 hours after tapping.

INTRODUCTION

One of the most important silvicultural problems in the pine forests of the world is the variable susceptibility of pines to their bark-beetle enemies. Wherever foresters have managed pine stands more intensively, they have become cognizant of the continuous depletion of their resource by bark beetles. Much of this drain could be prevented if foresters could recognize beetle-susceptible trees before they were killed. In some cases it has proved possible to recognize susceptible trees on the basis of morphological criteria alone (Keen and Salman, 1942; Keen, 1943). However, in most cases it is not possible to determine which trees are susceptible. An understanding of the fundamental basis for host susceptibility would facilitate the recognition of susceptible trees. Only with such knowledge can potential victims of the beetle be identified.

Logically, the initial question might be posed: what is the nature of bark-beetle resistance? Painter (1951, p. 27) discussed this question in his excellent book on the subject of insect resistance. He proposed two terms to categorize the mechanisms which jointly are responsible for resistance:

> "Preference or non-preference is used to denote the group of plant characters and insect responses that lead to or away from the use of a particular plant or variety, for oviposition, for food, or for shelter, or for combinations of the three. . . . The term anti-biosis is here used in its usual sense as the tendency to prevent, injure, or destroy [insect] life. . . ."

Thus, two fundamental questions to be considered in studying host susceptibility are: (1) what mechanisms govern the insect's preference for certain trees, and (2) what mechanisms govern the relative success of their attacks on susceptible versus resistant trees.

Investigators in California have expended a considerable amount of effort without successfully answering the first of these two questions. It will suffice to say that there is no demonstrable evidence in support either of the theory of olfactory selection advanced by Person (1931) or of the random attack hypothesis advanced by the writer[1].

Regardless of the existing inability to isolate the mechanisms responsible for host preference, an answer to the second of the two questions posed above would be of importance. It would provide silviculturists with a means of determining which trees would succumb to insect attack; hence, susceptible trees could be removed from a stand before they were killed. It also would provide tree breeders with information essential to the development of pines resistant to bark beetles.

What then might be the factors governing the success of bark-beetle attacks? Certainly, after bark beetles land on the bark of a pine tree which they have selected, the first factor in the attack sequence is the stimulus which provokes them to bore into the bark. It is unlikely that this initial stimulus varies

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1/ R.Z. Callaham, Host selection and host susceptibility in the western pine beetle-ponderosa pine complex. Manuscript Report. California Forest and Range Experiment Station. 1952.

according to the susceptibility of the tree. Dendroctonus and Ips beetles bore into the bark of both resistant and susceptible trees alike, when they are forced to attack such trees. When the beetles finally bore through the last layer of corky bark, they rupture the living phloem tissue. This tissue contains many resin ducts. At this point typically there is a flow of oleoresin from the severed resin ducts. The beetles must remove this material from their galleries; otherwise, they would suffocate in the mass of oleoresin which would completely engulf their bodies.

The duration of this struggle for survival is dependent upon the oleoresin production potential of the host and the energy potential of the insects. Whichever potential is exhausted first determines whether the beetles can continue their attack. The insects gain little or no nutrient from the phloem until the flow of oleoresin ceases. If the beetles survive the flow of oleoresin, they continue their attack. Providing the necessary stimuli and nutrients are available, the beetles proceed to construct galleries in the phloem. The galleries expose the xylem to air, and the attacking beetles incidentally inoculate the xylem with fungi. The final result is disruption of conduction which results in the death of the tree (Caird, 1935). In most cases a concentration of successful attacks, which survive the flow of oleoresin, results in the death of the tree.

Western forest entomologists continually notice in the field unsuccessful attacks on ponderosa pines, Pinus ponderosa Laws. These commonly occur on trees adjacent to individuals killed by bark beetles. Such attacks are characterized by abnormally large pitch tubes2/. These attacks are described as "pitched out." Insects making these abnormally large pitch tubes have often been observed to work a week or more in removing the oleoresin from their galleries before they die or abandon the attack. Conversely, in the case of successful attacks, the pitch tubes are small or occasionally absent entirely. In these cases of attacks on susceptible trees, the flow of oleoresin stops within a few days after the attack is initiated, or it never flows at all.

One might hypothesize then that the ability of a pine tree to produce oleoresin is the first critical factor governing its resistance to bark-beetle attacks. The tree's ability to produce oleoresin would include both the potential amount of production and the potential duration of production.

A review was made of the literature pertaining to the general resistance of pines to bark beetles. Many investigators have recognized the general importance of oleoresin production as a resistance mechanism. In the writings of von Tubeuf (1908, p. 406; 1933, p. 355) there was an early recognition of the importance of oleoresin exudation as a resistance mechanism. However, von Tubeuf was of the opinion that the turgor pressure within the stem governed the oleoresin exudation and was the critical factor in the resistance of conifers to their beetle enemies. Hopkins (1909, p. 64) in his monograph of the genus Dendroctonus wrote:

> "Some of the physiological features common to the species of this genus, and more or less peculiar to them, are found . . . in their habit of attacking living trees, in their concentration

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2/ Pitch tubes are accumulations of oleoresin, insect frass, and boring dust on the bark surface at the point of attack. They are formed as the beetles push the exuded oleoresin out of the entrance gallery.

of effort to overcome the resistance exerted by the tree attacked, and especially by their ability to manipulate and to dispose of the quantities of resin which flow into their burrows. . . ."

In 1930 Ivanov wrote:

> "Concerning many insect pests, especially bark beetles, the gum plays largely a mechanical role. Every time a resin duct is opened, the viscous gum is poured out with a force, covering the insect and killing it. Ips tridentatos when surrounded by a mass of fresh gum died in two minutes. If, however, the beetle is just smeared with the gum, it does not die. This explains the large infection of dry pines because at each disturbance of the water content, the resin pressure is reduced and the excretion of gum is weakened."

Büsgen and Münch (1931, p. 155) recognized:

> "the significance of resin in the life of the tree is that of a protective substance. . . . Fluid resin effectively wards off insects as it flows out under pressure when a resin duct is accidentally injured, overwhelms the attacker and kills it . . . Without /this resin protection/ the tree would be exposed to many more enemies, and perhaps, indeed, would be quite incapable of surviving in the face of our animal world."

More recently Keen (1952, p. 130), discussing bark-beetle ecology, wrote:

> "Dead and dying trees offer little resistance to attack and for this reason they are usually chosen by the secondary species that are not capable of coping with a vigorous pitch flow. Light attacks by primary species on living trees often fail because the flow of pitch is so copious that the attacking beetles are overcome or driven from their galleries. The oleoresins are known to be repellent and toxic to the beetles and so aid in resisting light attacks."

Becker (1951) studied the epidemic killing of pines by Dendroctonus species in Guatamala. He also recognizedthe importance of oleoresin as a resistance mechanism.

Several research workers have perceived the importance of oleoresin exudation with respect to the resistance of a specific pine to a given bark beetle. Struble[3/] studied the resistance of sugar pine, P. lambertiana Dougl., to the mountain pine beetle, Dendroctonus monticolae Hopk. He concluded:

> "The defense mechanism of the host tree against attacks is the resin which oozes slowly from wounded living tissue. The

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3/ G.R. Struble. Summary of investigative and control work on the mountain pine beetle in sugar pine stands of California. Manuscript Report. California Forest and Range Experiment Station. 1945.

> amount of resin which exudes varies greatly among different sugar pines attacked. . . . The speed and success of attacks depends on the amount of resin exuding and the ability of the beetles to eventually overcome it. Trees growing in a fairly dense stand are quickly overcome. In Struble's studies during 1933 every pole-size sugar pine tree in this type of stand on which beetles were forced to attack, through caging technique, were overcome within less than 10 days, with little evidence of resistance. In later studies during 1934 Struble attempted to induce attacks on the basal trunk portion of two mature trees and found that 'great resistance on the part of both trees was evident by resin flows so heavy that the bark surfaces were completely covered. Many attacks were attempted, none of which was successful, even to the point of starting an egg gallery. . . .' These studies indicated definitely that some sugar pines are capable of surviving the attacks as long as they are able to supply the quantities of resin necessary to resist the beetles. A deficiency in resin or the eventual exhaustion of this protective substance as a result of persistent beetle attacks quickly determines the fate of the host tree."

Anderson (1948) studied the selection of jack pines, P. banksiana Lamb., by the pine engraver, Ips pini (Say). He reported:

> "It was easy to induce Ips pini to attempt an attack even on vigorous trees by attracting the beetles to the trees with newly infested logs. Some of the attracted beetles attempted to attack the trees, but after they reached the inner bark they all stopped boring and vacated the tunnels. None was trapped in the resin."

Polozhentsev (1951) recognized the importance of oleoresin exudation as a resistance mechanism for Scots pine, P. sylvestris L. He developed a system of tapping with measurement of the subsequent oleoresin exudation to determine the relative health of individual trees and entire stands.

An analogous situation with respect to the eight-spined spruce bark beetle, Ips typographus L., attacking European spruce forest, has been recognized and investigated. Schwerdtfeger in two articles (1948, 1948a) stated: "These observations /of the resin flow in response to beetle attacks on standing and fallen trees/ show clearly, that spruce in this situation is able to resist bark-beetle attack through resin flow." He further noted that the resistance of the tree, based on resin flow, and the attack potential of the insect are not absolute, but rather they both change with changes in the environment. Reckman (1949, p. 58) has echoed this hypothesis.

The foregoing empirical evidence, which was obtained primarily from observation of attacks, lends support to the original hypothesis that oleoresin production is a critical factor governing host resistance. If the proposed hypothesis were correct, one might expect to find that susceptible trees would not have as great a capacity for oleoresin production as resistant trees. An investigation was undertaken to determine the oleoresin production potential of ponderosa pines resistant and susceptible to some California bark beetles. The susceptibility of individual ponderosa pines to some of the California bark beetles can be estimated in the field. On this basis trees of varying susceptibility were selected and

studied with respect to their olecresin production potential. It was anticipated that additional information in confirmation of the proposed hypothesis would be procured from these studies. Certainly, the absolute validity of the hypothesis could not be established, for the establishment of a correlation between susceptibility and ability to produce oleoresin would not establish that the rate of oleoresin production determines susceptibility. To establish causation one would have to subject bark beetles experimentally to different amounts of oleoresin production.

The following sections discuss the three primary investigations which were carried out. The first of these investigations included measurements of the daily rate at which oleoresin flowed from ponderosa pines of different insect susceptibility. These trees had been classified from morphological criteria as to their susceptibility to the western pine beetle, Dendroctonus brevicomis Lec. Measurements of flow rate also were made on other trees in the spring, when trees are considered to be resistant to engraver beetles, Ips spp. The latter trees were used for measurements again in the fall, when susceptibility to engraver beetles is considered to be higher. The final investigation involved a post-mortem examination of young trees attacked by the mountain pine beetle, Dendroctonus monticolae Hopk. The pitch tubes formed during attack by this insect on resistant and susceptible individuals were compared gravimetrically.

As these primary flow rate studies were undertaken, data were collected simultaneously for an analysis of the factors which were responsible for variations in flow rate. Items analyzed in this regard were: viscosity of the oleoresin, the size and number of ducts through which it flows, and the growth rate of the tree.

INVESTIGATIONS OF VARIATION IN OLEORESIN FLOW

Three investigations were undertaken to determine whether variations in the oleoresin production potential of individual trees could be correlated with the bark-beetle susceptibility of these trees. The best estimate of oleoresin production potential was considered to be a direct measurement of exudation from wounds under uniform conditions. Tree susceptibility had to be evaluated from the criteria presently available. In some cases the criterion of susceptibility was a tree classification. In other cases it was the observation of the success of actual attacks.

FLOW RATE IN SUSCEPTIBILITY TO THE WESTERN PINE BEETLE

The western pine beetle is the most important enemy of ponderosa pine. Average annual loss from this insect amounts to one billion b.f. or 0.5 percent of the total volume of ponderosa pine sawtimber. This loss occurs primarily in the large old-growth trees of poor vigor. Forest entomologists in California have found that this insect can be controlled best by removing the susceptible trees before they can be killed. This procedure is called sanitation-salvage logging. It not only saves the timber which would otherwise be lost, but it also removes the insect's favored breeding grounds. This tends to prevent both the loss of timber and the buildup of the insects in epidemic proportions (Keen, 1952a, pp. 688-694).

Forest entomologists have developed two systems of tree classification for recognizing susceptible trees. The accuracy of these systems has already been

established in the interior ponderosa pine type, Type 237 of the Society of American Foresters (1945). The first system, developed by Keen (1936, 1943), classifies trees by their age and thrift. The system is described and depicted in table 1 and figure 1. This system has value primarily as a silvicultural tool. Through its use one can determine the classes of trees which will be most susceptible in the long interval between harvest cuts. Many thousands of case histories have shown that the western pine beetle prefers the individuals which are the oldest (classes 3 and 4) and the least thrifty (classes c and d). The second system was developed by Salman and Bongberg (1942). This system classifies trees according to four degrees of current health as shown in table 2 and figure 2. It is used as a silvicultural tool for the purpose of stand sanitation. Using this system, one can rate individual trees with respect to the risk of their succumbing to bark-beetle attack within a short term of five to ten years. These two classification systems offer the best available methods of estimating western pine beetle susceptibility. Nevertheless, it should be emphasized, neither of these classifications is absolute. For example Keen4/ reports from one study that only 30% of the Risk 4 trees were killed in a ten-year period following rating.

The Experiment

Trees classified according to Keen class and risk rating should provide the best base for determining whether the oleoresin production potential of a tree is correlated with its susceptibility to the western pine beetle. Accordingly, such trees were selected in virgin interior ponderosa pine stands. They were tapped over a period of several days. The amount of oleoresin which exuded each day was determined gravimetrically. A statistical analysis then was made to determine whether trees of different age classes, vigor classes, or risk ratings produced significantly different amounts of pitch each day. A similar analysis also was made to determine whether the trees differed in the duration of their oleoresin production.

On the basis of previous turpentining experience (Mirov, 1930; Schopmeyer and Larson, 1954), one logically would expect the best oleoresin production from the largest, fastest-growing, most full-crowned trees. These trees would be in the younger age classes, 1 and 2, in the better vigor classes, a and b, and in the lower risk ratings, 1 and 2.

Experimental Trees

The trees used in this study were located on plots 1-3. The location and description of these plots is given in table 3. The plots were established in virgin stands of the Blacks Mountain Experimental Forest by J.W. Bongberg of the Berkeley Forest Insect Laboratory. Every tree on each plot was permanently numbered. A written description of the morphological characteristics of each tree was prepared. The Keen class and risk rating were noted, and they were revised periodically. The final descriptions were made in 1947 by J. W. Bongberg, an authority on such classification. The particular trees used in this study also were redescribed during the investigation by F. P. Keen.

4/ F. P. Keen. Ponderosa pine tree characteristics indicative of high risk to pine beetle attack. Manuscript Report. California Forest and Range Experiment Station. 1954.

The study trees were selected from written plot records before going to the areas. Only 50 trees could be sampled at one time; hence, an attempt was made to select a uniform distribution of trees with respect to age classes, to vigor classes, and to risk ratings. This was not always possible because trees of young age, low vigor, and high risk were not available in the desired numbers. Table 4 shows the distribution of tree classes used in this study as determined by Bongberg in 1947 and by Keen in 1953. In general, these two men agreed as to each tree's Keen class; however, there are discrepancies in their rating of risk. The latter may be the result of personal differences in rating the trees. In this case, however, there is considerable reason to believe that the trees actually have improved in risk in the interval between ratings5/. The photographs in figure 3 show a tree which apparently has improved in risk and one which has remained as it was in 1947.

Collection of Data

In studying the rate of flow of oleoresin, one must ensure that a uniform wound, uniform collection device, and uniform time interval are used in all measurements. In this study each tap was made with a brace and 1½-inch wood bit. The tip screw-thread on the bit had been removed flush with the cutting lips (figure 4) to prevent breaking the wood surface. The collection device which was used (figure 4) was a modified Gilmer apparatus. Its basic design was suggested by C. S. Schopmeyer, Research Forester, Southeastern Forest Experiment Station, Lake City, Florida. The collection device in the form of a reducing "L" was constructed of black extruded butyrate plastic tubing. One end was sealed with a disc of frosted acrylic plastic. A cork was slipped over the side arm to hold an 8-dram vial in which the oleoresin collected. The time interval used in most studies was 24 hours. All weighings were made to the nearest 0.01 gram on a torsion balance. The balance was placed in a wind shelter atop a plane table (figure 5).

Ideally all flow rate measurements should be made at the same time under identical environmental conditions. However, with the manpower and equipment which were available, it was not possible to work more than 50 trees at a time. First a small study limited to a few trees was undertaken to develop procedures. Then approximately 50 trees on each of three plots were studied in succession. This resulted in 166 trees being tapped during a six-week period extending from the middle of June to the end of July. Figure 6 shows the dates of tapping and the weather conditions prevailing at the local weather station6/.

5/ M. M. Furniss, A photographic study of the change of insect risk in ponderosa pine. Manuscript Report. California Forest and Range Experiment Station. 1954.

6/ The weather station is located at Blacks Mountain Experimental Forest Headquarters, which is approximately five miles from the experimental area, within the same timber type, and at an elevation of 5600 feet above sea level.

TABLE 1

DESCRIPTION OF KEEN'S TREE CLASSES

AGE CLASSES

CLASS 1

YOUNG TREES. COMMONLY REFERRED TO AS "BULL PINES" OR "BLACK JACKS"; THRIFTY TREES MAKING RAPID HEIGHT AND DIAMETER GROWTH; AGE USUALLY LESS THAN 80 YEARS.

D.B.H.--RARELY OVER 20 INCHES.

HEIGHT.--IN LOWER CROWN CANOPY; USUALLY LESS THAN 60 PER CENT OF TOTAL MATURE HEIGHT.

BARK.--DARK, GRAYISH BROWN TO BLACK; ROUGH, AND DEEPLY FURROWED WITHOUT PLATES, BUT WITH NARROW RIDGES BETWEEN THE FISSURES (SOMETIMES COLORING AT EXTREME BASE).

BRANCHES.--UPTURNED AND IN WHORLS FOR UPPER THREE-FOURTHS OF CROWN; SMALL FOR DIAMETER OF BOLE.

TOP.--USUALLY POINTED, WITH DISTINCT WHORLS.

CLASS 2

IMMATURE TREES. STILL MAKING RAPID HEIGHT AND DIAMETER GROWTH IN THRIFTY TREES; AGE APPROXIMATELY 80 TO 180 YEARS.

D.B.H.--RARELY OVER 30 INCHES.

HEIGHT.--USUALLY LESS THAN 90 PER CENT OF TOTAL HEIGHT AT MATURITY. TREES STILL UNDER THE GENERAL CROWN CANOPY.

BARK.--DARK REDDISH BROWN, WITH NARROW, SMOOTH PLATES BETWEEN THE FISSURES ON LOWER HALF OF BOLE; DARK, ROUGH BARK ON UPPER HALF.

BRANCHES.--MOSTLY UPTURNED AND IN WHORLS FOR UPPER HALF OF CROWN; HORIZONTAL NEAR MIDDLE, HORIZONTAL OR DROOPING BELOW; SMALL TO MEDIUM SIZE FOR DIAMETER OF BOLE.

TOP.--USUALLY POINTED, SOMETIMES ROUNDED, BUT WITH WHORLS INDISTINCT.

CLASS 3

MATURE TREES. HEIGHT GROWTH PRACTICALLY COMPLETE; DIAMETER GROWTH SLOW; AGE APPROXIMATELY 180 TO 300 YEARS.

D.B.H.--RARELY OVER 40 INCHES.

HEIGHT.--PRACTICALLY THAT OF THE GENERAL CROWN CANOPY, EXCEPT INTERMEDIATE, SUPPRESSED, OR TOP-KILLED TREES.

BARK.--LIGHT REDDISH BROWN WITH MODERATELY LARGE PLATES BETWEEN THE FISSURES ON LOWER THREE-FOURTHS OF BOLE; DARK BARK SHOWING IN UPPER QUARTER.

BRANCHES.--UPTURNED NEAR TOP, MIDDLE CROWN HORIZONTAL, LOWER ONES DROOPING; MODERATELY LARGE FOR SIZE OF BOLE.

TOP.--USUALLY PYRAMIDAL OR ROUNDED, OCCASIONALLY POINTED; WHORLS INDISTINCT EXCEPT AT EXTREME TOP.

CLASS 4

OVERMATURE TREES. MAKING NO FURTHER HEIGHT GROWTH; DIAMETER GROWTH VERY SLOW; AGE MORE THAN 300 YEARS.

D.B.H.--WIDE LATITUDE IN DIAMETERS, BUT USUALLY LARGE IN DOMINANT TREES.

HEIGHT.--FULL HEIGHT OF GENERAL CROWN CANOPY, EXCEPT SUPPRESSED, SPIKE-TOPPED, OR BROKEN TREES.

BARK.--LIGHT YELLOW AND UNIFORM FOR ENTIRE BOLE, EXCEPT IN EXTREME TOP; PLATES USUALLY VERY WIDE, LONG, AND SMOOTH; FISSURES OFTEN RATHER SHALLOW.

BRANCHES.--LARGE, HEAVY, AND OFTEN GNARLED OR CROOKED; MOSTLY DROOPING EXCEPT IN EXTREME TOP.

TOP.--USUALLY FLAT; OCCASIONALLY ROUNDED OR IRREGULAR.

CROWN-VIGOR CLASSES

CLASS A

FULL VIGOR

CROWN.--FULL VIGOROUS CROWNS WITH A LENGTH OF 55 PER CENT OR MORE OF THE TOTAL HEIGHT, AND OF AVERAGE WIDTH OR WIDER; WITH DENSITY AVERAGE OR BETTER, FOR ITS AGE CLASS.

FOLIAGE.--NEEDLES OF AVERAGE LENGTH OR LONGER, USUALLY DENSE AND THRIFTY.

POSITION.--USUALLY ISOLATED OR DOMINANT, RARELY CODOMINANT.

D.B.H.--LARGE FOR AGE.

CLASS B

GOOD TO FAIR VIGOR

CROWN.--GOOD TO MODERATELY VIGOROUS CROWNS, WITH LENGTH FROM 30 TO 55 PER CENT OF TOTAL HEIGHT, IF OF AVERAGE WIDTH AND DENSITY; OR A LONGER CROWN IF NARROW OR SOMEWHAT THIN; BUT NEITHER SPARSE NOR RAGGED.

FOLIAGE.--NEEDLES OF AVERAGE LENGTH, USUALLY DENSE AND THRIFTY.

POSITION.--USUALLY CODOMINANT, BUT SOMETIMES ISOLATED OR DOMINANT; RARELY INTERMEDIATE.

D.B.H.--AVERAGE OR ABOVE FOR AGE.

CLASS C

FAIR TO POOR VIGOR

CROWN.--FAIR TO POOR CROWNS, WITH LENGTH FROM 10 TO 30 PER CENT OF TOTAL HEIGHT IF OF AVERAGE WIDTH AND DENSITY, OR LONG, SPARSE, AND NARROW; OFTEN FLAT ON ONE OR MORE SIDES.

FOLIAGE.--NEEDLES OFTEN SHORT AND THINLY DISTRIBUTED, BUT OF NORMAL LENGTH AND DENSITY WHEN CONFINED TO TOP ONE-THIRD OF CROWN.

POSITION.--USUALLY INTERMEDIATE, SOMETIMES CODOMINANT OR SUPPRESSED, BUT RARELY ISOLATED.

D.B.H.--USUALLY BELOW AVERAGE FOR AGE; SOMETIMES LARGE IN DECADENT TREES.

CLASS D

VERY POOR VIGOR

CROWN.--VERY SHORT, LESS THAN 10 PER CENT OF THE TOTAL HEIGHT; SOMETIMES MERELY A TUFT AT TOP OF TREE, OR SOMEWHAT LONGER WHEN SPARSE AND RAGGED; USUALLY VERY NARROW OR LIMBS ALL ON ONE SIDE.

FOLIAGE.--NEEDLES OFTEN SHORT, AND FOLIAGE SPARSE OR SCATTERED, OR ONLY TUFTS AT END OF TWIGS; BUT OF NORMAL LENGTH AND DENSITY IF REDUCED IN QUANTITY.

POSITION.--USUALLY SUPPRESSED OR INTERMEDIATE, BUT MAY OCCUPY OTHER POSITIONS IF GREATLY REDUCED IN VIGOR.

D.B.H.--DECIDEDLY SUBNORMAL FOR AGE, BUT VERY OLD DECADENT TREES MAY BE OF LARGE DIAMETER.

AGRICULTURE FOREST SERVICE, SAN FRANCISCO

Fig. 1.--

A PONDEROSA PINE TREE CLASSIFICATION

BASED ON AGE AND VIGOR

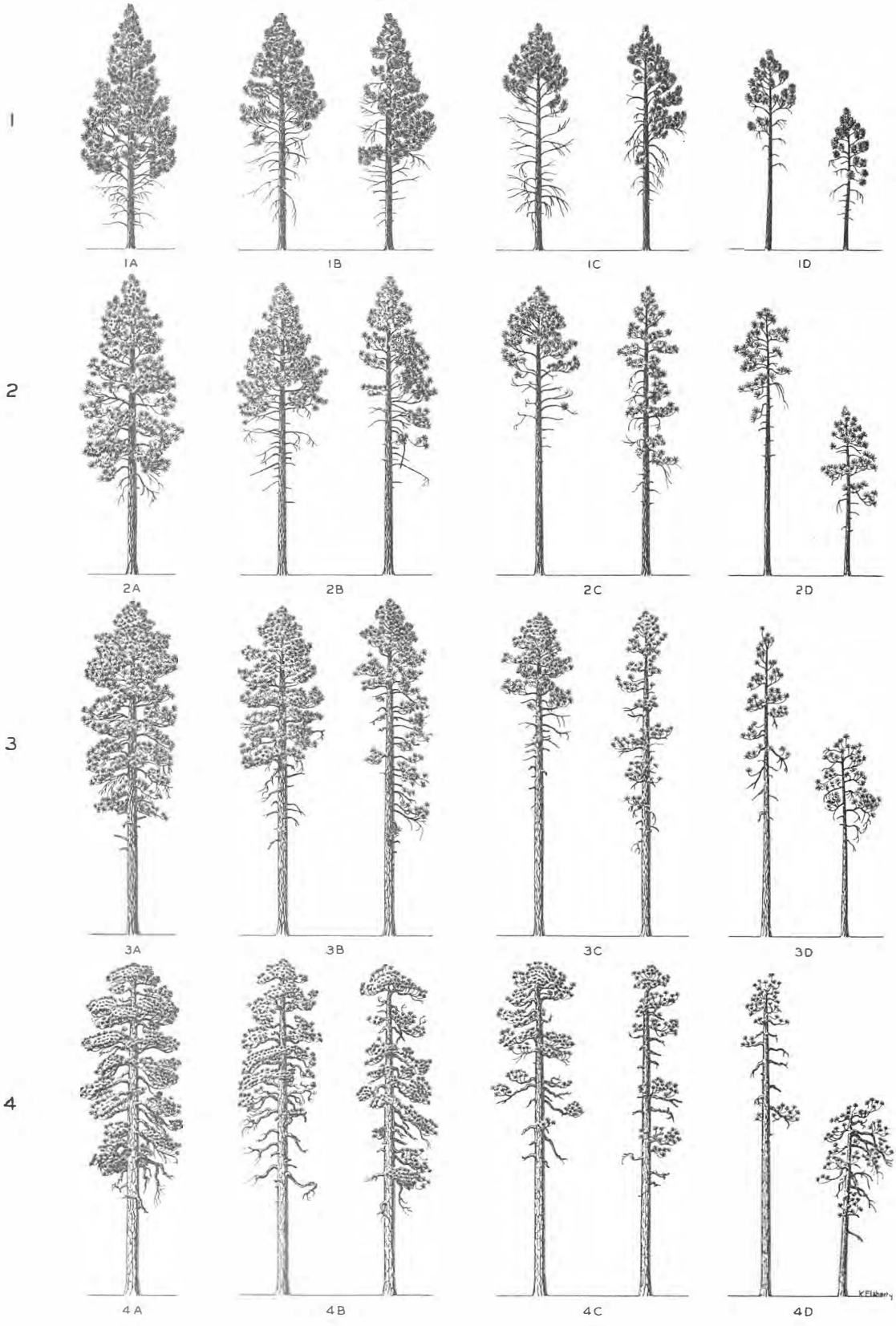


Table 2.—Description of risk ratings (Anon., 1951)

Risk 1. Low Risk

Full foliaged, healthy appearing crowns. Foliage of healthy appearance, needles usually long and coarse, color good dark green. Practically all twigs with normal foliage complement. No weakened portions of crown.

Risk 2. Moderate Risk

Fair to moderately healthy crowns, imperfect in spots. Foliage mostly healthy, needle length average or better, color fair to good. Some twigs or branches may lack foliage, but such injury should not be localized to form definite "weak" spots in crown.

Risk 3. High Risk

Crowns of fair to poor health, somewhat ragged or thin in portions of crown. Foliage in parts of crown thin, bunchy, or unhealthy, needles average to shorter than average in length, color fair to poor. Some to many twigs or branches lacking foliage, some to many twigs or branches fading or dead. Small localized weakened portions of crown usually present.

Risk 4. Very High Risk

Crowns in poor condition, ragged or thin, often showing evidence of active insect infestations in upper portions. Foliage thin or bunchy, needles short or sparse, color poor. Twigs and branches dead or dying, portions of crown definitely weakened. Active topkilling or partial infestations often present.

Fig. 2

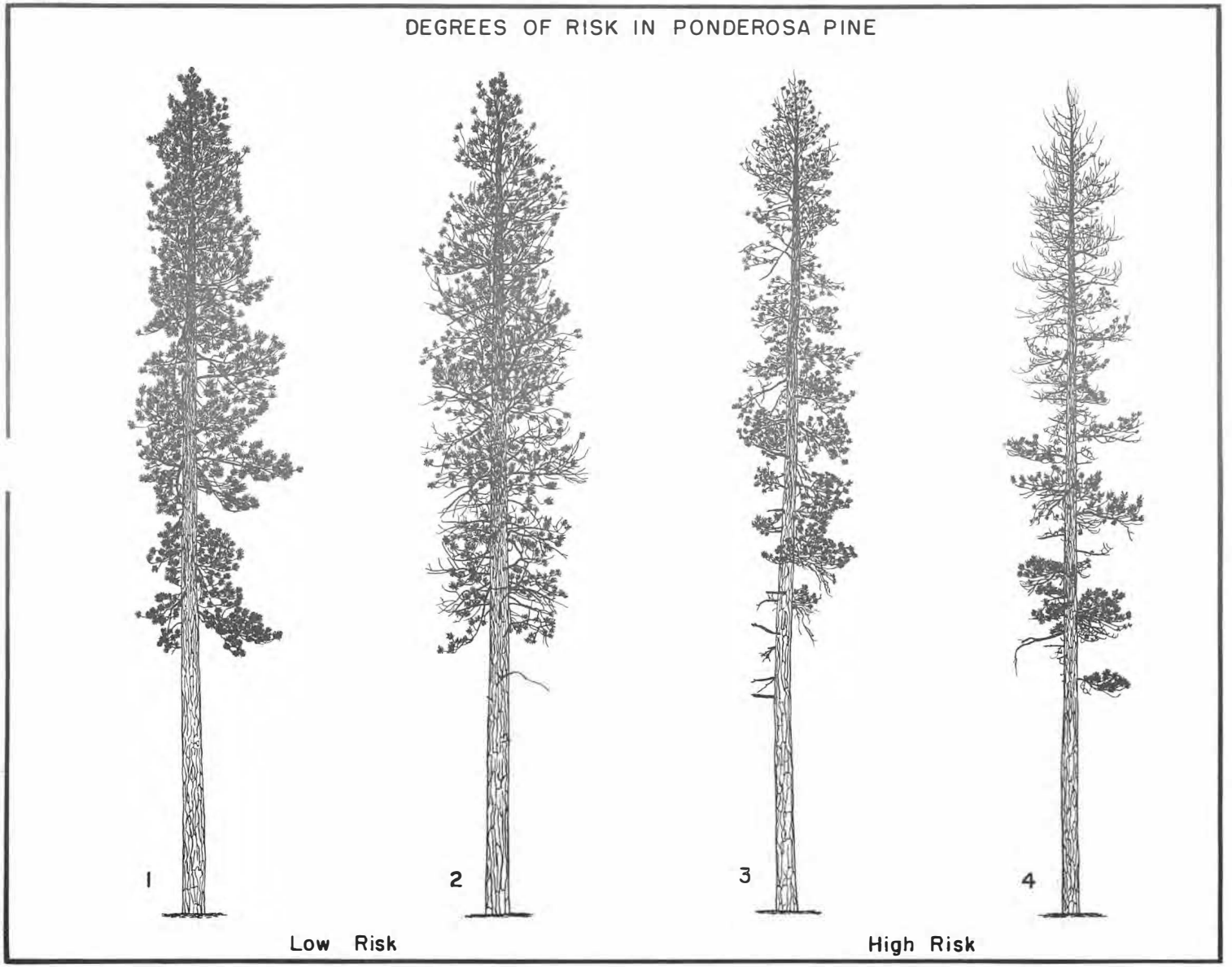


Table 3.—Location and description of experimental plots

No.	Location	Description
1	Lassen Co., Sec.7, T 33 N, R 8 E. Compartment P 21-28, Blacks Mtn. Exp. Forest	Virgin, gentle southwest slope of Patterson Mtn., Elev. 6000 ft.
2	Lassen Co., Sec.23, T 33N, R7E Compartment G2-12, Blacks Mtn. Exp. Forest	Virgin, flat, Elev. 5700 ft.
3	Lassen Co., Sec.11, T33N, R7E, Compartment A 21-10, Blacks Mtn. Exp. Forest	Virgin, flat island of pine on rocky outcrop in large meadow, Elev. 5700 ft.
WB-2	Shasta Co., Sec.11, T36N, R3E	Heavy Forest Service Cut in 1943. Flat on west rim of Lake Britton, Elev. 2800 ft.
CL-21	Shasta Co., Sec. 30, T34N, R4E	Virgin, mixed conifer, flat, Elev. 4700 ft.

Table 4.—Distribution of tapped trees by tree class, Blacks Mountain Experimental Forest, 1953

Age Class	Bongberg 1947	Keen 1953	Vigor Class	Bongberg 1947	Keen 1953	Risk Rating	Bongberg 1947	Keen 1953
1	14	16	a	60	56	1	87	89
2	33	27	b	47	56	2	35	52
3	57	61	c	47	41	3	19	20
4	62	62	d	12	13	4	25	5

Figure 3. — Changes in risk — 1946 to 1953.

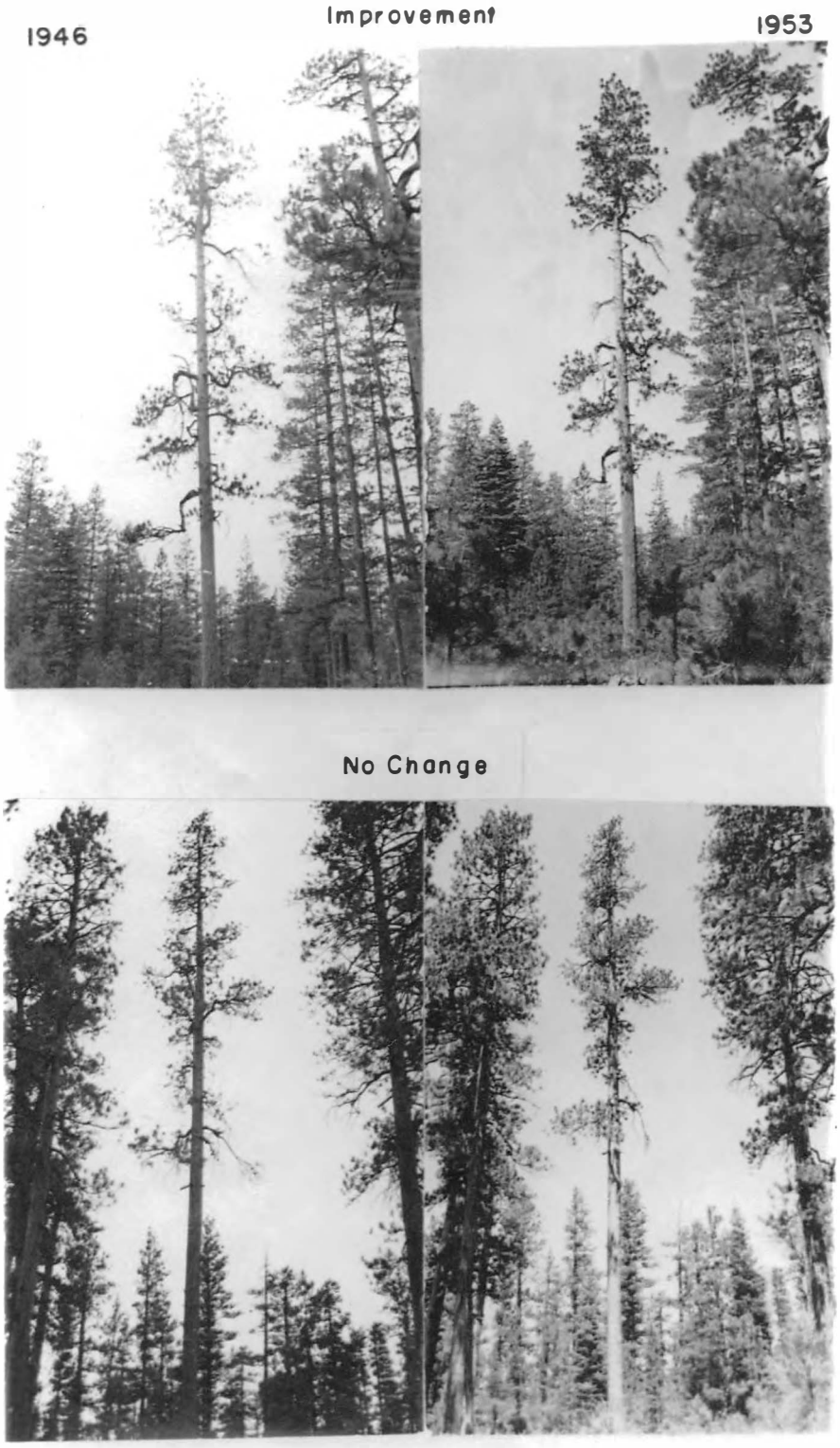


Figure 4.—The tapping instruments and collection device.

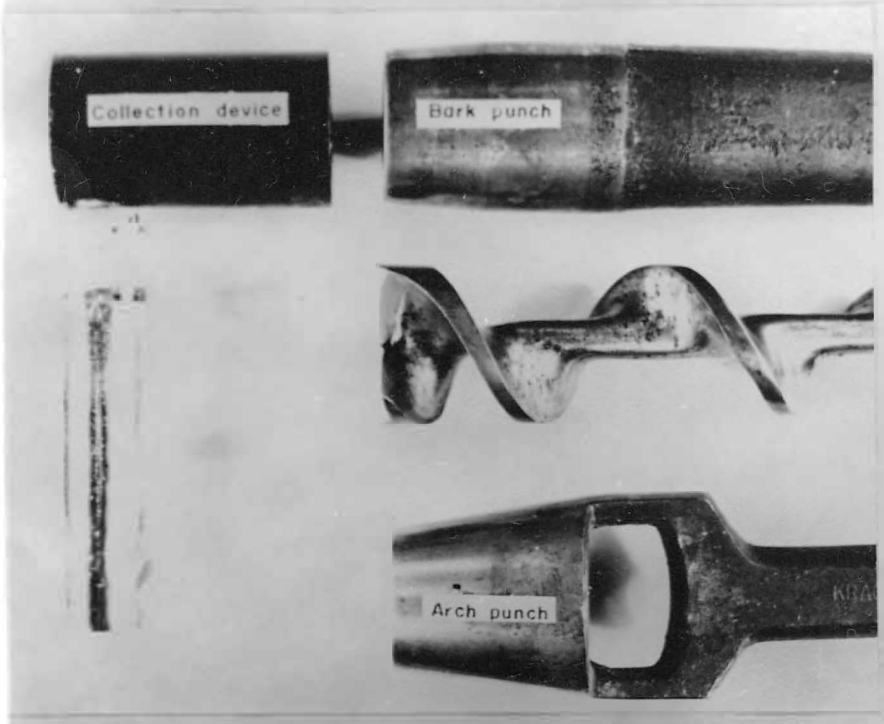
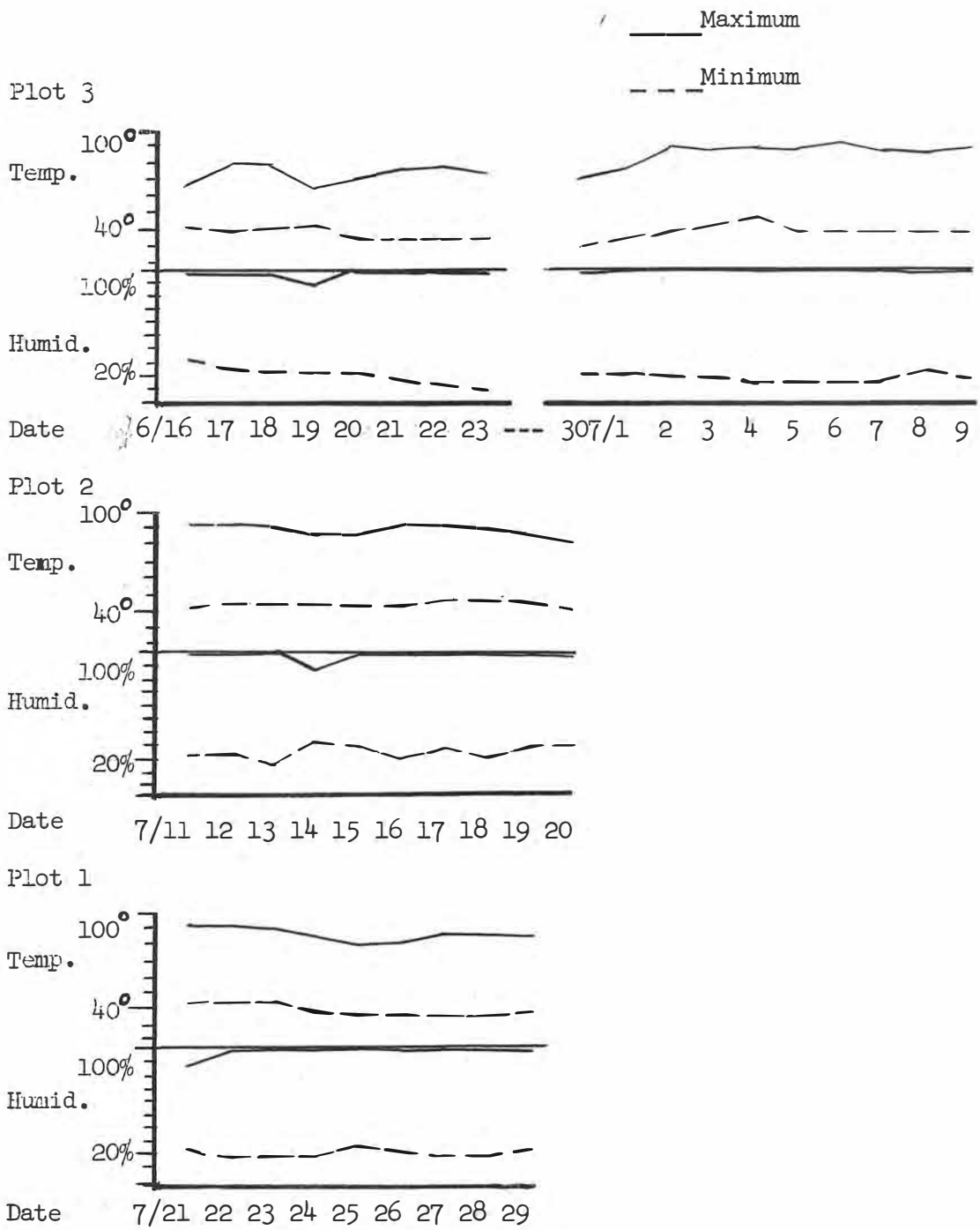


Figure 5.—The balance next to a tapped tree.

Figure 6.--Dates of tapping and prevailing weather conditions[1], Blacks Mountain Experimental Forest, 1953.



1/ There was no precipitation during the tapping periods.

Before tapping was started on each plot, the collection devices were dried in an oven and weighed. The weight was written in pencil on the frosted end. The receiving vials also were labeled, numbered, dried, and weighed. The weight was entered on the vial label.

The first day on each plot was devoted to tapping the trees and installing the collection devices. The selected trees were tapped at breast height. A space on each of the four cardinal sides of each tree was smoothed with an axe, and the north face of each tree was marked with "N." A hole was bored with the brace and bit at each smoothed space (figure 7). The holes were bored just through the corky bark into the phloem. Then a knife was used to sever the phloem at the edges of the bore. When this had been done, the phloem was scraped away from the wood surface. Care was taken at all times to avoid rupturing the wood surface. The open end of the collection device was inserted into the bore hole and pressed tightly against the wood surface. It was wedged in place with a bark chip. The time of working to the nearest five minutes was entered on a form for each tree.

The second and succeeding days were expended in weighing the vials with the accumulating oleoresin. A plane table was placed in the center of a group of trees which had been tapped. The table was leveled; the balance was placed in its shelter and adjusted. The four vials were collected from each tree in the order in which the trees had been tapped. The position of each vial was noted on its label. The vials were weighed (figure 8), and the weight and time were entered in the notes with the vial number, tare, and position. The vials then were returned to their proper positions on the tree (figure 9).

On the final day the vials were weighed as before. In addition the collection devices were removed and weighed. The weight of the oleoresin accumulated therein was determined and entered in the notes. All of the vials of oleoresin were corked, sealed with "Duco" cellulose acetate cement, and placed in refrigeration. The collection devices were washed and rinsed in cleaning solvent, were oven-dried, and were weighed again before re-use.

Analysis of Data

The field data were transcribed on punch cards for machine computation and tabulation. First the mean flow per wound was obtained for each tree on each day. In some cases the time interval between weighings was not exactly 24 hours. The corrected mean flow per wound for each day was derived by multiplying the actual mean flow by a suitable correction factor[7/]. A card was punched for each tree bearing the plot number, tree number, tree class both by Bongberg and by Keen, and corrected mean flow for each day. These daily flow rates were accumulated by machine to give the cumulative flow on each day. Next, the cumulative flow rates were squared by machine. Finally,

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7/ The correction factors used were derived on the basis of a uniform, constant flow rate during any 24-hour period. This assumption had to be made because hourly flow rate curves were not available for accurate estimates of the proportion of flow occurring during a given interval of any 24 hour period. A maximum error of ten percent could have been introduced with discrepancies of two hours. However, such cases were encountered only infrequently.

the cumulative flow rates and their squares were summed by age class, vigor class, and risk rating. This provided the data necessary for variance analyses of the amount of oleoresin produced by trees differing in their susceptibility to the western pine beetle.

Further machine computations were made to provide data on the duration of flow. Only in a few cases had the flow of oleoresin ceased before the collection devices were removed. For this and other reasons, duration of flow had to be analyzed in terms of the successive daily decreases in amount of oleoresin produced. The cumulative flow for each day was divided by the cumulative flow for the preceding day. This gave each day's flow as a percentage of the total preceding flow. These percent values were subjected to an arcsine transformation. The transformed values were punched in the cards, and their squares were computed by machine. Finally the transformed values and their squares were summed by age class, vigor class, and risk rating. This provided the information necessary for a variance analysis of differences in the duration of flow of oleoresin from susceptible and resistant trees.

The data derived from all of these machine summations were subjected to analyses of variance. A one-way classification with unequal size classes was used throughout[8/]. The following statistical test was used throughout:

$$F = \frac{\frac{(n-p)}{(p-1)}\left[\sum_i Sn_i \bar{x}_i^2 - n\bar{x}^2\right]}{SSX_{ij}^2 - \sum_i Sn_i \bar{x}_i^2}$$

where p = the number of classes ($i = 1, 2, \ldots p$),

n_i = the number of items (X_{ij}) ($j = 1, 2, \ldots n_i$) in class i,

giving a total of $n = \sum_i Sn_i$ observations.

$\bar{x}_i$ = mean of all observations in class i,

$\bar{x} = \sum_i Sn_i \bar{x}_i$ = grand mean of all n observations.

The Results

Amount of Flow

From the data in table 5a there was no reason to believe that trees of different age classes or vigor classes produced different cumulative amounts of oleoresin. This was true during the first eight days after tapping. This did not substantiate the original hypothesis of less flow in classes comprised of slower-growing, smaller-crowned individuals. An extremely large variance in the amount of oleoresin produced by different trees within each age and vigor class was not evaluated in the one-way analyses which were conducted. Nevertheless, this variance within classes included in the "Error"

8/ The formula for the analysis of variance was supplied by Dr. Joseph Putter, Statistical Laboratory, University of California, Berkeley.

component of variance, undoubtedly was important in obscuring differences between classes. The extent of the variance in oleoresin production due to individual tree differences within classes is indicated in figure 10.

The last column of table 5a shows that the trees with different risk ratings, as determined by Keen in 1953, produced significantly different amounts of oleoresin. Yet, trees similarly classified by Bongberg in 1947 did not show such significant differences. Table 5b shows the number of trees sampled and the mean cumulative flow rate for each risk rating on successive days. T tests were made to determine whether there were significant differences between particular means. Table 5c shows the results of these tests. During the entire tapping period, the risk 2 individuals produced less oleoresin than did any of the others. On three of the eight days this was a significant difference. The data provide a significant basis on which to refute the null hypothesis of differences in amount of flow between risk ratings; however, there also is a possibility that an error of the first kind exists. Thus, in an error of the first kind the data might show a significant difference disproving the null hypothesis when the null hypothesis of no differences actually is valid.

With respect to trees of the other three risk ratings, there does not appear to be much difference in the amount of oleoresin excreted. There is one minor exception in the significant difference between risk one and risk four trees on the first day after tapping. Certainly, there is no consistent increase or decrease in amount produced by more susceptible trees.

It would appear then that the study of age classes, vigor classes, and risk ratings did not produce any evidence in support of the hypothesis that susceptible trees produce less oleoresin than do resistant trees. Neither is there any convincing evidence in support of the reciprocal hypothesis that resistant trees produce less oleoresin than do susceptible trees.

The foregoing statistical tests were refined further by selecting the trees used in each variance analysis. Specifically, in analyses for differences in the amount of oleoresin produced by trees of different age classes, the only trees used were those of good vigor, a's and b's, and of low risk, risk 1. In the analyses of differences in vigor classes, the trees used were those of ages 2, 3, and 4 and of risk 1. Only the trees of ages 3 and 4 and good vigor were used in comparing risk ratings.

Only trees of the selected classes were used in the analyses summarized in table 6a. This table is similar in plan and results to table 5a except for the trees used as a base. Table 6a shows as before that there were no significant differences between age or vigor classes in the cumulative production of oleoresin. The extreme variability in quantity of oleoresin produced by individual trees of the same class is depicted in figure 10. Table 6a does show that during the first two days after tapping there was a significant difference in the amount of oleoresin produced between trees of different risk ratings. As in table 5, only the trees rated by Keen in 1953 showed such significance. Table 6b shows the numbers of individuals sampled and the mean cumulative flow observed in each risk rating. In table 6c the means of different risk ratings are compared. Again only the very low flow of risk 2 trees was significantly different.

Figure 7. – Tapping a tree with brace and bit.

Figure 8 – Weighing the vials of oleoresin.

Figure 9. -- Collection device in position.

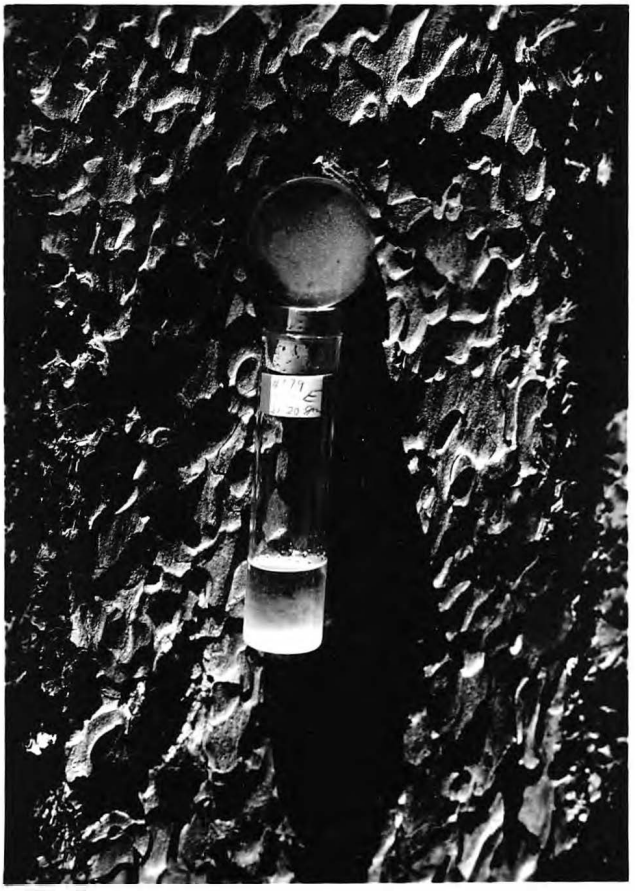

Table 5a.—F values from variance analyses of the cumulative amount of oleoresin produced up to eight days after tapping by trees[1/] of different age classes, vigor classes, and risk ratings

SOURCE OF VARIATION	df	AGE CLASSES classed in 1947	AGE CLASSES classed in 1953	VIGOR CLASSES classed in 1947	VIGOR CLASSES classed in 1953	RISK RATINGS rated in 1947	RISK RATINGS rated in 1943
Between classes 1 days' flow	3	.129	.165	.547	.791	.824	4.864 **
Error	155						
Between classes 2 days' flow	3	.289	.317	.421	.574	.329	2.605
Error	160						
Between classes 3 days' flow	3	.426	.339	.835	1.003	.034	.145
Error	160						
Between classes 4 days' flow	3	.471	.331	1.347	1.449	.107	.451
Error	161						
Between classes 5 days' flow	3	.357	.230	1.765	1.758	.223	2.814 *
Error	162						
Between classes 6 days' flow	3	.585	.392	1.354	1.333	.260	2.549
Error	161						
Between classes 7 days' flow	3	.532	.295	1.850	2.104	.381	2.521
Error	151						
Between classes 8 days' flow	3	.360	.296	1.588	1.880	.481	2.766 *
Error	140						

1/ All trees tapped in 1953 were used in these analyses regardless of their classes other than the one under consideration.

* Variance due to differences in amount of flow between classes is significant at the .05 probability level.

** Variance is significant at the .01 probability level.

Table 5b.—The number of individuals per risk rating and mean cumulative oleoresin flow

Cumulative Flow Days	Risk Ratings	All Trees Rated in 1947 n	All Trees Rated in 1947 mean	All Trees Rated in 1953 n	All Trees Rated in 1953 mean
1 days' flow	1	85	4.74	86	5.12
	2	33	4.76	50	3.94
	3	17	5.50	18	6.22
	4	24	5.79	5	8.54
2 days' flow	1	87	7.42	88	8.11
	2	34	7.40	51	5.99
	3	19	7.76	20	9.00
	4	24	8.68	5	10.76
3 days' flow	1	87	9.45	88	10.24
	2	34	9.12	51	7.13
	3	19	9.19	20	10.90
	4	24	9.68	5	11.27
4 days' flow	1	87	10.54	89	11.24
	2	35	9.69	51	7.67
	3	19	9.86	20	11.81
	4	24	10.07	5	11.40
5 days' flow	1	87	11.09	89	11.77
	2	35	10.00	52	7.78
	3	19	10.15	20	12.30
	4	25	9.89	5	11.43
6 days' flow	1	87	11.41	89	12.10
	2	35	10.20	50	8.14
	3	18	10.66	20	12.55
	4	25	9.99	6	9.57
7 days' flow	1	82	12.10	84	12.76
	2	33	10.57	47	8.48
	3	16	11.30	19	12.72
	4	24	10.29	5	11.44
8 days' flow	1	79	12.36	82	12.91
	2	31	10.72	43	8.74
	3	12	13.51	15	15.13
	4	22	10.70	4	11.26

Table 5c.-- T values from tests of the significance of differences between means of cumulative flow of oleoresin on days on which variance analyses had shown significant differences between risk ratings

	Comparing Risks					
	1 and 2	1 and 3	1 and 4	2 and 3	2 and 4	3 and 4
1 days' flow	2.51 *	.87	2.15 *	1.78	2.88 *	1.17
	(134)1/	(102)	(89)	(66)	(53)	(21)
5 days' flow	3.30 **	0.21	0.12	1.85	1.36	0.25
	(139)	(107)	(92)	(70)	(55)	(23)
8 days' flow	3.11 **	0.68	0.47	2.10 *	0.73	0.86
	(123)	(95)	(84)	(84)	(45)	(17)

1/ Degrees of freedom

* Difference between means is significant at the .05 probability level.

** Difference is significant at the .01 probability level.

Figure 10. -- Examples of the variation in cumulative oleoresin production for individual trees.

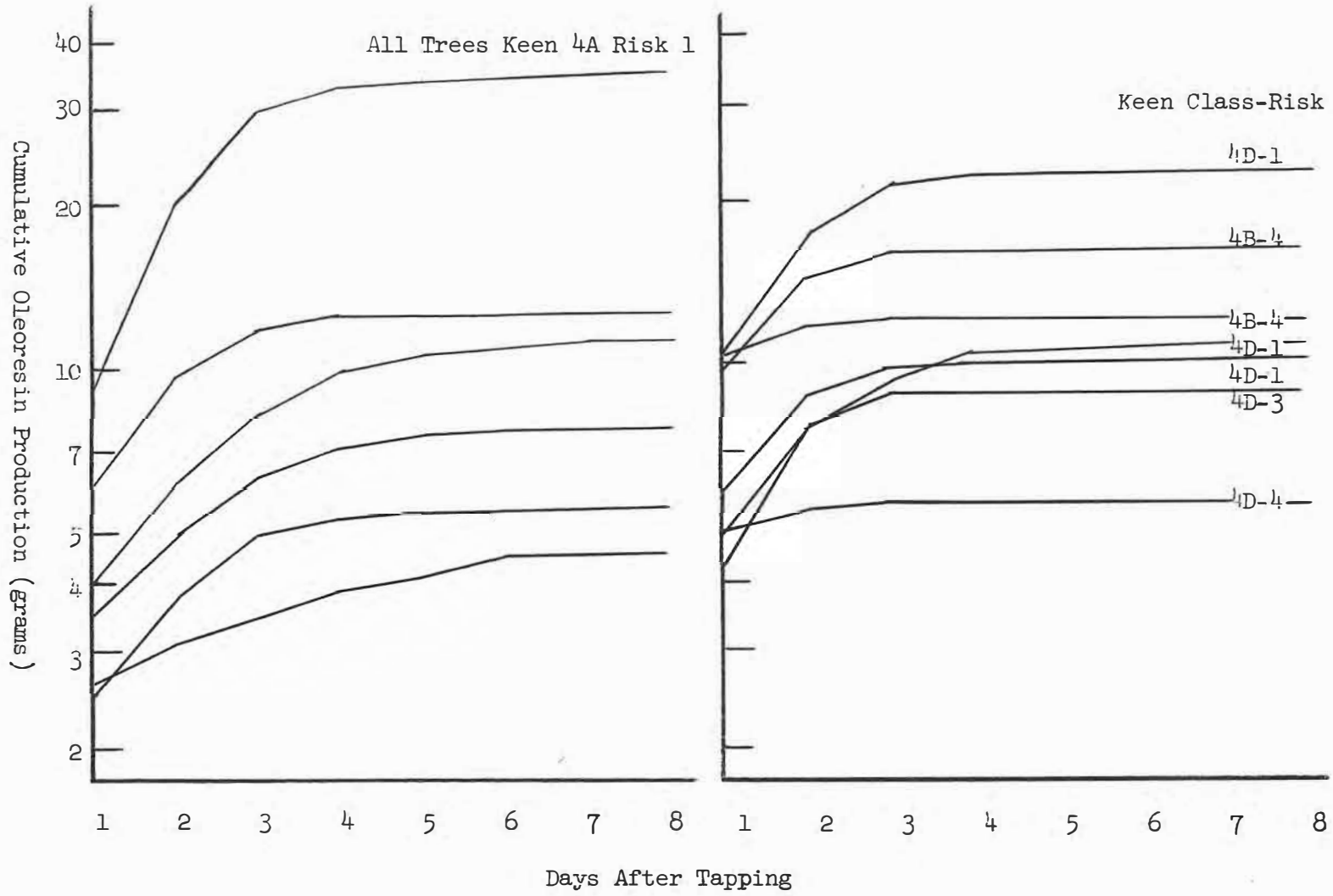

Table 6a.— F values from variance analyses of the cumulative amount of oleoresin produced up to eight days after tapping by selected trees 1/ of different age classes

SOURCE OF VARIATION	AGE CLASSES IN 1947 df	F	AGE CLASSES IN 1953 df	F
Between classes 1 days' flow	3	.689	3	.094
Error	75		62	
Between classes 2 days' flow	3	.272	3	.307
Error	75		62	
Between classes 3 days' flow	3	.093	3	.248
Error	77		63	
Between classes 4 days' flow	3	.109	3	.262
Error	77		63	
Between classes 5 days' flow	3	.102	3	.250
Error	77		63	
Between classes 6 days' flow	3	.096	3	.217
Error	77		63	
Between classes 7 days' flow	3	.119	3	.316
Error	73		59	
Between classes 8 days' flow	3	.078	3	.299
Error	70		57	

1/ Trees tapped in 1953 and selected for this analysis were those with good vigor (a's and b's) and low risk (risk 1).

Table 6a (continued).- F values from variance analyses of the cumulative amount of oleoresin produced up to eight days after tapping by selected trees2/ of different vigor classes

SOURCE OF VARIATION	VIGOR CLASSES IN 1947 df	F	VIGOR CLASSES IN 1953 df	F
Between classes 1 days' flow	3	1.908	3	1.981
Error	68		68	
Between classes 2 days' flow	3	.837	3	1.099
Error	68		68	
Between classes 3 days' flow	3	.871	3	.821
Error	70		70	
Between classes 4 days' flow	3	.817	3	.839
Error	70		70	
Between classes 5 days' flow	3	1.523	3	.749
Error	70		71	
Between classes 6 days' flow	3	.613	3	.824
Error	70		71	
Between classes 7 days' flow	3	.678	3	.972
Error	65		66	
Between classes 8 days' flow	3	.779	3	1.023
Error	63		65	

2/ Trees tapped in 1953 and selected for these analyses were those with ages 2, 3, and 4 and risk 1.

Table 6a (continued).— F values from variance analyses of the cumulative amount of oleoresin produced up to eight days after tapping by selected trees of different risk ratings3/

SOURCE OF VARIATION	RISK RATINGS IN 1947		RISK RATINGS IN 1953	
	df	F	df	F
Between classes 1 days' flow	3	1.507	3	3.887 *
Error	62		73	
Between classes 2 days' flow	3	.813	3	2.899 *
Error	62		73	
Between classes 3 days' flow	3	.252	3	1.939
Error	65		76	
Between classes 4 days' flow	3	.200	3	1.994
Error	65		76	
Between classes 5 days' flow	3	.197	3	2.081
Error	65		76	
Between classes 6 days' flow	3	.138	3	2.275
Error	66		77	
Between classes 7 days' flow	3	.322	3	1.941
Error	60		70	
Between classes 8 days' flow	3	.247	3	2.521
Error	56		64	

3/ Trees tapped in 1953 and selected for these analyses were those with ages 3 and 4 and good vigor (a's and b's).

* Variance due to differences in amount of flow between classes is significant at the .05 probability level.

Table 6b.—The number of selected individuals sampled and the mean cumulative flow in each risk rating

Cumulative Flow Days	Risk Rating	Risk Ratings Selected Trees Rated in 1947 n	mean	Rated in 1953 n	mean
1 days' flow	1	33	5.29 gms.	36	4.90 gms.
	2	17	4.29	28	4.00
	3	9	7.00	9	8.19
	4	6	7.36	3	8.35
2 days' flow	1	33	8.86	36	8.64
	2	17	7.09	28	6.06
	3	9	10.86	9	13.30
	4	6	11.32	3	10.67
3 days' flow	1	35	10.75	37	10.91
	2	17	9.41	29	7.20
	3	10	11.69	10	14.64
	4	6	13.08	3	11.16
4 days' flow	1	35	12.14	37	12.24
	2	17	10.35	29	7.83
	3	10	12.70	10	16.14
	4	6	13.86	3	11.23
5 days' flow	1	35	12.82	37	12.88
	2	17	10.73	29	8.07
	3	10	13.13	10	16.94
	4	6	14.25	3	11.25
6 days' flow	1	35	13.12	37	13.20
	2	17	10.99	29	8.16
	3	10	13.30	10	17.36
	4	7	12.39	4	8.49
7 days' flow	1	32	14.30	34	14.23
	2	16	11.35	26	8.72
	3	10	13.39	10	17.54
	4	5	16.57	3	11.26
8 days' flow	1	31	14.49	33	14.42
	2	14	11.75	24	8.75
	3	9	14.49	8	20.74
	4	5	16.60	2	10.80

Table 6c. T values from tests of the significance of differences between means of cumulative flow of oleoresin on days on which variance analyses had shown significant differences between risk ratings

	Comparing Risk					
	1 and 2	1 and 3	1 and 4	2 and 3	2 and 4	3 and 4
1 days' flow	1.23	1.45	1.84	1.89	2.40 *	0.06
	(62)1/	(43)	(37)	(35)	(29)	(10)
2 days' flow	1.80	1.33	0.66	2.19 *	1.61	0.61
	(62)	(43)	(37)	(35)	(29)	(10)

1/ Degrees of freedom

* Difference between means is significant at the .05 probability level.

Even with the refinements introduced in this analysis there was a general lack of consistent significant differences in the amount of pitch produced by trees of different age and vigor classes and risk ratings. Thus the data failed to support the hypothesis that individual ponderosa pines, recognized as being resistant to the western pine beetle, have the potential to excrete a greater amount of oleoresin than susceptible individuals.

Duration of Flow

Perhaps the significance of oleoresin in resistance was the time of exudation and not the total amount of exudate. This possibility was investigated with the data on duration of flow.

It was necessary to analyze for diminishing flow rather than for absolute duration of flow. This was requisite because very few trees had stopped producing oleoresin during the eight-day period of tapping. Consequently, the analyses were made using the daily increments of oleoresin as a measure of flow diminution. Each day's flow was expressed as the percent of the cumulative flow through the preceding day. The differences between age classes, vigor classes, and risk ratings were considered on the basis of all trees which were tapped. Further considerations of age, vigor, and risk were made on the basis of a sample of trees selected as for the foregoing study of amount of flow.

The analyses of differences between vigor classes and risk ratings showed significant differences in daily flow percent through the seventh and eighth days after tapping. The results of the variance analyses made on the data from all tapped trees are presented in table 7a. Table 7b shows the number of individuals and mean daily flow for each age class, vigor class, and risk rating on each day. T tests were not made to determine the significance of differences between these mean values; nevertheless, observation alone showed that there was a general marked reduction in percent daily flow for trees of poor vigor classes and high risk ratings. On the other hand, the analyses of differences between age classes showed decreasing flow in older classes, but the differences between classes were not significant except on the sixth day after tapping. It is possible that bias was introduced into these analyses which used all trees. The poor vigor and high risk trees were found almost exclusively in the older age classes. Similarly the high risk trees generally were trees of poor vigor.

A selected sample of trees was used for an analysis of age class differences in daily flow. When good vigor, low risk trees were so analyzed (table 8a), there was no evidence to refute the null hypothesis. Thus, one must conclude that there were no significant differences between age classes in the duration of oleoresin production. In this way the bias introduced into the age class comparisons in table 7a through the use of all tapped trees was eliminated.

When comparable bias was removed from the vigor class comparisons in table 8a, it was evident that there was little or no evidence to refute the null hypothesis except on the fourth day after tapping. On that day table 8b shows that there was a significant decrease in flow in the poor vigor classes as compared with the good vigor classes.

Table 7a.—F values from variance analyses of the daily flow of oleoresin for the third through the eighth days after tapping by trees of different age classes, vigor classes, and risk ratings[1]

SOURCE OF VARIATION	df	AGE CLASSES classed		VIGOR CLASSES classed		RISK RATINGS rated	
		in 1947	in 1953	in 1947	in 1953	in 1947	in 1953
Between classes 3rd day flow	3	1.089	0.138	4.466**	2.852*	6.443**	6.333**
Error	160						
Between classes 4th day flow	3	1.223	1.472	9.713**	8.881**	8.640**	5.538**
Error	160						
Between classes 5th day flow	3	1.883	1.407	7.126**	6.199**	5.859**	6.619**
Error	161						
Between classes 6th day flow	3	4.046**	3.480*	6.081**	6.322**	5.483**	3.541*
Error	159						
Between classes 7th day flow	3	0.483	0.454	5.883**	3.001*	3.680*	2.678*
Error	150						
Between classes 8th day flow	3	0.312	0.217	3.746*	1.884	3.222*	1.693
Error	140						

1/ All trees tapped in 1951 were used in these analyses regardless of their classes other than the one under consideration.

* Variance due to difference in amount of flow between classes is significant at the .05 probability level.

** Variance is significant at the .01 probability level.

Table 7b.—The number of individuals in each age class and the mean daily flow for the third through the eighth days after tapping

DAY OF FLOW	AGE CLASS	DAILY FLOW AS PERCENT INCREASE IN TOTAL AMOUNT CLASSIFIED IN 1947		CLASSIFIED IN 1953	
		n	mean	n	mean
3rd	1	14	18.6 gms.	16	20.1 gms.
	2	33	24.0	27	22.1
	3	56	22.3	60	21.5
	4	61	18.6	61	20.1
4th	1	14	10.9	16	11.6
	2	33	8.1	27	7.0
	3	56	7.2	60	6.8
	4	61	6.5	61	7.2
5th	1	14	4.7	16	4.7
	2	33	3.8	27	3.4
	3	56	2.6	60	2.6
	4	62	2.5	62	2.7
6th	1	14	3.9	16	3.8
	2	33	2.0	27	1.5
	3	55	1.3	59	1.4
	4	61	1.3	61	1.4
7th	1	14	0.93	16	0.87
	2	32	0.79	26	0.49
	3	52	0.67	55	0.76
	4	56	0.53	57	0.60
8th	1	13	0.19	15	0.18
	2	31	0.35	25	0.24
	3	50	0.26	53	0.26
	4	50	0.24	51	0.30

Table 7b (continued).—The number of individuals in each vigor class and the mean daily flow for the third through the eighth days after tapping

DAY OF FLOW	VIGOR CLASS	DAILY FLOW AS PERCENT INCREASE IN TOTAL AMOUNT CLASSIFIED IN 1947		CLASSIFIED IN 1953	
		n	mean	n	mean
3rd	a	60	24.2 gms.	56	25.7 gms.
	b	47	24.3	56	19.2
	c	45	15.2	40	19.0
	d	12	15.4	12	14.6
4th	a	60	10.1	56	11.1
	b	47	9.2	56	7.3
	c	45	4.2	40	4.8
	d	12	2.8	12	2.6
5th	a	60	4.3	56	4.6
	b	47	3.3	56	2.8
	c	46	1.6	40	1.8
	d	12	1.3	13	1.4
6th	a	60	2.5	56	2.8
	b	46	1.7	55	1.2
	c	45	0.79	39	1.1
	d	12	0.74	13	0.69
7th	a	58	0.79	53	1.1
	b	43	1.2	52	0.65
	c	41	0.23	37	0.39
	d	12	0.25	12	0.21
8th	a	54	0.33	49	0.43
	b	41	0.45	48	0.23
	c	37	0.08	35	0.16
	d	12	0.15	12	0.15

Table 7b (continued).—The number of individuals in each risk rating and the mean daily flow for the third through the eighth days after tapping

DAY OF FLOW	RISK RATING	DAILY FLOW AS PERCENT INCREASE IN TOTAL AMOUNT RATED IN 1947		RATED IN 1953	
		n	mean	n	mean
3rd	1	87	24.0 gms.	88	23.2 gms.
	2	34	22.3	51	18.1
	3	19	20.1	20	24.9
	4	24	10.2	5	2.7
4th	1	87	9.6	88	9.0
	2	34	7.3	51	5.8
	3	19	6.4	20	7.6
	4	24	2.3	5	0.56
5th	1	87	3.9	89	3.8
	2	35	2.6	51	1.9
	3	19	2.4	20	3.5
	4	24	1.0	5	0.10
6th	1	86	2.2	89	1.9
	2	35	1.5	49	1.3
	3	18	1.1	20	1.6
	4	24	0.46	5	0.02
7th	1	82	0.93	84	0.84
	2	33	0.62	47	0.50
	3	16	0.51	18	0.71
	4	23	0.14	5	0.00
8th	1	79	0.38	82	0.33
	2	31	0.26	43	0.20
	3	12	0.11	15	0.22
	4	22	0.06	4	0.00

Table 8a.— F values from variance analyses of the daily flow of oleoresin for the third through the eighth days after tapping by selected trees[1/] of different age classes, vigor classes, and risk ratings

SOURCE OF VARIATION	AGE CLASSES 1953		VIGOR CLASSES 1953		RISK RATINGS 1953	
	df	F	df	F	df	F
Between classes 3rd day flow	3	1.297	3	1.586	3	4.886**
Error	70		77		89	
Between classes 4th day flow	3	0.279	3	3.314*	3	6.222**
Error	70		77		89	
Between classes 5th day flow	3	0.135	3	1.640	3	7.551**
Error	70		78		89	
Between classes 6th day flow	3	2.077	3	1.406	3	3.028*
Error	69		77		86	
Between classes 7th day flow	3	0.736	3	0.863	3	2.020
Error	65		72		81	
Between classes 8th day flow	3	0.341	3	0.068	3	0.923
Error	61		69		69	

1/ Trees tapped in 1953 and selected for age analyses were those with good vigor (a's and b's) and low risk (risk 1); for vigor analyses were those with ages 2,3, and 4 and risk 1; for risk analyses were those with ages 3 and 4 and good vigor (a's and b's).

* Variance due to difference in amount of flow between classes is significant at the .05 probability level.

** Variance is significant at the .01 probability level.

Table 8b.—The number of selected individuals in each class and the mean daily flow in grams for the third through the eighth days after tapping

DAY OF FLOW	DAILY FLOW AS PERCENT INCREASE IN TOTAL AMOUNT								
	AGE			VIGOR			RISK		
	Class	n	mean	Class	n	mean	Rate	n	Mean
3rd	1	12	18.3	a	32	28.9	1	45	26.9
	2	17	25.7	b	30	24.2	2	33	22.6
	3	31	28.6	c	13	24.4	3	12	32.7
	4	14	23.3	d	6	14.7	4	3	1.9
4th	1	12	10.2	a	32	10.9	1	45	11.1
	2	17	9.2	b	30	10.2	2	33	7.4
	3	31	11.5	c	13	6.0	3	12	11.4
	4	14	10.1	d	6	3.4	4	3	0.49
5th	1	12	5.1	a	32	4.4	1	45	4.4
	2	17	4.1	b	30	4.3	2	33	2.2
	3	31	4.5	c	13	2.8	3	12	5.8
	4	14	4.2	d	7	1.6	4	3	0.09
6th	1	12	4.2	a	31	2.4	1	44	1.9
	2	17	2.0	b	30	1.5	2	31	1.5
	3	30	2.1	c	13	1.6	3	12	2.8
	4	14	1.4	d	7	0.71	4	3	0.03
7th	1	12	1.0	a	29	1.0	1	41	1.2
	2	16	0.63	b	28	1.1	2	29	0.68
	3	28	1.4	c	13	0.57	3	12	0.63
	4	13	0.88	d	6	0.24	4	3	0.00
8th	1	11	0.26	a	27	0.40	1	38	0.45
	2	16	0.27	b	27	0.39	2	25	0.35
	3	26	0.46	c	13	0.34	3	8	0.23
	4	12	0.44	d	6	0.28	4	2	0.00

The most interesting fact, however, was that a similar treatment of the data for risk rating comparisons to remove age and vigor bias did not affect the highly significant decrease in flow. Of course, the possibility still exists that there has been committed an error of the first kind, refuting the null hypothesis when it is actually correct. However, it may be concluded fairly reliably that the very high risk trees showed a considerably diminished flow from the third through the sixth day after tapping.

Discussion

This investigation demonstrated that there was a tremendous variation between trees in total production of oleoresin during the first eight days after tapping. Considering the magnitude of this variance, it was not surprising that significant differences between tree classes in amount of exudation could not be demonstrated. However, this fact does not disprove the original hypothesis that the susceptibility of an individual tree to the western pine beetle is determined by the amount of oleoresin which it produces.

The analyses indicated further that there was no significant change in the amount of oleoresin produced as trees become either older or less thrifty. At least, this seemed to be the case with respect to flow during the first eight days after tapping. From this one might conclude that maturity and vigor do not enter into the determination of a tree's quantitative oleoresin production potential. Of course, in the last analysis the observed differences in cumulative flow must be explained in terms of the interaction of different genetic constitutions (Mergen, 1953) and environmental conditions for each tree.

The discovery that the rate of flow diminishes more rapidly in certain types of susceptible trees is of primary importance. What is the significance of this finding in the bark-beetle problem? One possibility is that the attacking insect can persist in its attack regardless of the quantity of oleoresin exuding into its gallery during the first few days. Yet, the beetles only can undertake gallery excavation in the phloem if the flow of oleoresin diminishes rapidly or actually ceases before the energy of the beetles is expended. It is more difficult to conceive of why the flow should diminish more rapidly in certain trees. Perhaps diminishing flow is due to the reduction in the synthesis of more oleoresin to refill the resin ducts as their contents are discharged; or perhaps it is due to a reduction in the internal pressures which cause the oleoresin to be excreted; or perhaps it is due to the rapid sealing of the ends of the severed ducts with crystalline oleoresin.

There is a need for additional investigation of the relationship between susceptibility and the amount and duration of oleoresin flow. In recognition of the large variation in flow between trees, it is obvious that such an investigation should be extended to a large number of trees. The number should be far in excess of the 166 individuals used in this particular study. Such a large scale investigation should be designed to determine for each tree the mean flow per tree during the first two days after tapping and the following two days. All tapping would have to be completed in a short time to give comparable data for all trees. The data collected should serve over the next few years as a relative measure of each tree's ability to produce

oleoresin. All of the trees so tapped would have to be observed in annual surveys to determine actual mortality. Thus, actual long-term mortality experience would provide data on susceptibility for correlation with oleoresin production potential. Amount of oleoresin flow actually may be more closely correlated with susceptibility than was indicated by the correlations with tree class and risk rating. Only mortality experience will establish this point.

Annual observations of mortality of the trees tapped in 1953 are underway already. Two of these trees died late in 1953. One tree, a Risk 4 individual, which did not produce any oleoresin whatsoever, was newly infested at the time it was tapped. The second tree, Risk 3, was far below normal in its oleoresin production. More of this kind of data may eventually establish the value of the proposed hypothesis.

Another experimental approach, which might be utilized in future studies, is the use of forced attacks. Trees morphologically similar but considerably different in their ability to produce oleoresin could be caged and subjected to heavy bark-beetle attacks. The validity of the hypothesis under study might be established more readily from such attacks than from the long, drawn-out period required for mortality experience to accumulate.

FLOW RATE IN SUSCEPTIBILITY TO THE ENGRAVER BEETLE

The pine engravers, Ips spp., are another important group of beetles throughout the pine forests of the world. In contrast to the Dendroctonus beetles, the economic importance of this group is more difficult to assess. Certain kinds of material seem to be most susceptible to these insects. Their usual breeding places are slash, windfalls, and other down timber. Under certain circumstances, notably drought conditions (Craighead, 1950, p.12; Schwerdtfeger, 1948, 1948a), they attack standing trees. They kill smaller trees both in the virgin forest and in the residual stands of unmerchantable trees left after logging. Furthermore, they characteristically attack the tops of larger trees. This top-killing of older trees may be important in rendering such trees susceptible to attack by other insects. Ultimately, the pine engravers may rank in importance with the Dendroctonus beetles as enemies of our pine stands. Certainly, in European forests Ips typographus L. is one of the most important enemies of coniferous trees (Reckman, 1949, p. 30).

Pine engravers kill trees in much the same way as do the Dendroctonus beetles. They usually make successful attacks in host materials which do not produce oleoresin at the point of their attacks. Their entrances characteristically lack pitch tubes, and the boring dust emitting from their entrances is not pitchy (Keen, 1952). They do not seem to be capable of attacking trees which produce oleoresin (Anderson, 1948; Schwerdtfeger, 1948). The presence or absence of oleoresin exudation possibly could be a factor governing the success of attacks on pines by certain species of Ips. Leach et al. (1934, p.338), conducted investigations with two species of Ips. They stated: "Many bark beetles are known to attack living trees most successfully when the trees are weakened by drought or other factors. It is very probable that reduced resin flow or moisture content of the inner bark may be the determining factor in such cases." Schwerdtfeger also expressed the opinion that the oleoresin

production capacity of European spruce definitely is related to its resistance to Ips typographus L. In general it appears that standing trees killed by Ips species actually may be "slash-on-the-stump" from a physiological point of view.

The California five-spined engraver, Ips confusus (Lec.) is a typical member of this genus. It is the most destructive pine engraver attacking ponderosa pine in California. The biology and ecology of this insect have been studied intensively in recent years by G.R. Struble and R.C. Hall, Entomologists, U.S. Forest Service9/. They have found that this engraver breeds in down material in the spring and early summer months. During late summer and fall, the emerging adults attack standing trees when conditions permit. Struble and Hall report Hall's finding: "There is some evidence that soil moisture and outbreaks of the pine engraver are related." They conclude: "Adequate soil moisture during the growing season is believed to be a key factor in building up resistance against attacks." With respect to individual trees, these workers suggest that host moisture deficiencies "may become more critical in the upper main stem, where attacks usually start, especially in trees larger than pole size." In consideration of these two points, one might conclude that susceptibility to this insect increases in the upper part of the bole in the fall season of certain dry years.

Let us return to the original hypothesis that oleoresin production potential is critical in determining susceptibility. If this hypothesis were valid, one might expect both that there would be less oleoresin produced in the upper parts of the boles and that therewould be less oleoresin produced in the fall season in certain dry years. Investigations were undertaken to determine the validity of both of these proposals. Several trees were tapped at regular intervals along the bole to determine differences in the rate of oleoresin flow. Another series of trees was tapped twice, once when soil moisture was high and again when soil moisture was low; differences in the rate of oleoresin exudation were measured both times.

Flow from Different Positions on Bole

There seem to be no previous studies of the influence of the height of the stem on the quantitative variation in oleoresin exudation. Ivanov (1930) reported that E.F. Votchal used manometers to measure gum exudation pressure at different positions on the bole. Votchal, apparently working with a species of pine in Russia, found that gum exudation pressure was lower in the tops of the trees than below. Gum exudation pressure undoubtedly plays an important role in the rate of gum exudation, but it would be difficult to predict variations in actual flow from variations in gum exudation pressure. In accord with the approach to determining oleoresin exudation potentials directly from measurements of actual oleoresin exudation rates, several ponderosa pines were tapped uniformly at various positions along their boles.

9/ G.R. Struble and R.C. Hall. The California five-spined engraver - serious enemy of reserve and second-growth ponderosa pine. Manuscript Report. California Forest and Range Experiment Station. 1954.

The Experiment

Experimental trees.— The trees used in this investigation were immature, vigorous, rapidly growing individuals. Their selection was governed in part by the proximity of the lower limbs to the ground. They were located on the grounds of the Institute of Forest Genetics, Placerville, California.

Collection of data.— A ladder was erected to the lowest limb of each tree. Each tree was climbed and was tapped at the four cardinal directional aspects at each of four levels on the bole. In all cases the uppermost tapping was made at a point where the bole was estimated to be ten inches in diameter. Subsequent tappings below this point were made at approximately twenty-foot intervals down the bole. The final tapping was done at breast height, $4\frac{1}{2}$ feet above ground.

Tapping in this study was done with a steel punch (figure 4) which was made to the exact outside diameter of the collection device. The punch was used to sever the bark, and the resulting bark core with the attached phloem was removed with a knife. The collection device was pressed into the wound, where it was held in place by friction. The amount of oleoresin exuding during the subsequent 24-hour interval was determined gravimetrically.

Analysis of data.— The field data were assembled for statistical analyses. The total flow for each wound was obtained. The corrected flow was derived through the use of a suitable correction factor[10/]. This was necessary only in the few cases where the time interval had not been exactly 24 hours.

Each tree was considered independently in the subsequent analyses. This was necessitated by the fact that the trees had not been selected randomly from the population of trees in the area. As the first step, variance analyses were made to determine the significance of differences both between heights and between directional aspects. Where significant differences between heights were found, "t" tests were carried out. The purpose of these "t" tests was to determine whether there was a significant difference in mean amount of flow between the top and bottom of each tree.

The Results

There did not seem to be a significant component of variance resulting from different directional aspects. On the other hand, the results of the analyses of height data indicate a significant decrease in flow from the bottom to the top of the tree. This was found in three of the four trees studied. Table 9a presents the results of the variance analyses to determine the significance of differences both between height and between aspects in the amount of exudation during the 24 hours following tapping. Table 9b shows the tests of significance of differences in mean amount of flow from the top

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10/ The correction factors used were derived on the basis of a uniform, constant flow rate during any 24-hour period. This assumption had to be made because hourly flow rate curves were not available for accurate estimates of the proportion of flow occurring during a given interval of any 24 hour period. A maximum error of $\pm$ ten percent could have been introduced with discrepancies of two hours. However, such cases were encountered only infrequently.

and bottom of the trees. The mean 24-hour flow of oleoresin for each position on each tree is plotted in figure 11. The curves all show a general increase in flow from top to bottom.

Flow in Different Seasons of the Year

Nearly all investigators of seasonal variation in oleoresin flow have found a generally increasing flow of oleoresin during the warm summer months. In fall decreasing yield has been found to be associated with falling temperatures and other factors. Specifically, for ponderosa pine in California, Mirov (1930) found a generally increasing flow of oleoresin during the summer until about the beginning of September. Thus, one should expect increasing flow during the critical late summer dry periods in normal years; whereas, according to the proposal in question, there should be less oleoresin produced in August and September in certain dry years. Ivanov reported that Votchal found a lower oleoresin exudation pressure during drought. The original work plan called for a test of the validity of the proposal; however, it could not be tested as desired. The growing season moisture was above average in 1953 when the study was undertaken. Nevertheless, a number of trees were tapped during periods of high and low soil moisture to determine differences in rate of oleoresin exudation in a year of good precipitation.

The Experiment

Experimental trees.— Two sets of trees were selected for the investigation of the seasonal differences in flow rate. Ten vigorous, thrifty, dominant or codominant trees were chosen for study on each of two plots. Each tree had been classified by J. W. Bongberg in 1947 as to Keen class and risk rating. The plots, LB-2 and CL-21 (table 3), are located in the vicinity of Hat Creek, Shasta County, California. These particular plots were chosen because of their past history. They were established by Hall during his study of the influence of climatic factors on bark-beetle behavior. Hall's records showed for these plots: the period of lowest soil moisture, the wilting point of the soil, and the relative hazard of bark-beetle loss (Johnson, 1949). The plot at Warner's bridge, WB-2, had a high bark-beetle hazard; the soil wilting point was 10.6 percent on a dry weight basis. The plot near Cornaz Lake, CL-21, had a low bark-beetle hazard; the wilting point of the soil was 7.2 percent. For both plots the period of lowest soil moisture was approximately September 1.

Collection of data.— Each of the selected trees was tapped in June and again late in August, 1953. Each tree was tapped with brace and bit at breast height on four sides: north, west, south, and east. The exposed wood surfaces then were sprayed with a 50 percent aqueous solution of sulphuric acid to stimulate oleoresin flow (Mirov and Kimbrough, 1952). The oleoresin which exuded during the next 24 hours was collected, and the amount was determined gravimetrically. The time interval between tapping and weighing was recorded to the nearest five minutes.

Soil moisture determinations were made at the time of each tapping. Eight to ten randomly located soil samples were taken on each plot at a depth of 9-12 inches. Moisture content was determined on a dryweight basis.

Analysis of data.— The data were accumulated by plots for each tapping. The total flow of oleoresin from each wound was obtained. From this

value the corrected flow per wound was derived. The mean flow per wound for each tree and for each plot then was computed. Finally, "t" tests were made to determine the significance of differences between plot means in June and August. The percent soil moisture and standard error also were calculated for each plot at both tappings.

The Results

All of the trees, regardless of plot, showed a higher flow rate in August than in June. The data are presented graphically in figure 12. T tests of the differences between mean flow in June and mean flow in August on each plot show these differences to be highly significant (table 10). These data support Mirov's results. They do not provide evidence for an evaluation of the proposal that there would be a reduced flow in the dry season of certain years with deficient growing season precipitation.

Originally, it was planned to test the significance of differences between plots at each tapping; however, climatic conditions were so dissimilar on the two plots as to make any such comparison invalid. At each tapping temperatures were much lower at the higher elevation plot, CL-21. Winds also were stronger and the sky more cloudy at the upper elevation plot.

Discussion

The investigation of oleoresin flow rate at different positions on the bole produced conclusive evidence that the amount of flow was far less in the upper portion of the bole than in the lower portion. Ips confusus and other pine engravers make their attacks on the upper portion of the bole. Thus, these beetles attack the portion at which they encounter the least amount of oleoresin. Such circumstantial evidence merely shows an association of the insect with a condition of the host; it does not constitute a verification of the general hypothesis that the success of bark-beetle attacks is governed by the oleoresin production of the host. A true cause and effect relationship has not been demonstrated.

The primary question remains unanswered: "Is oleoresin toxic to these insects." Studies of the toxicity of oleoresin to various species of pine bark beetles are urgently needed. Such studies might be made either by applying oleoresin directly to the insects or by forcing them to attack trees which vary in their oleoresin production capacity. If oleoresin could be shown to be toxic to these insects, then the information gleaned from this particular study would explain the attack pattern which the insects produce.

Table 9a.— Analyses of variance in 24-hour exudation of oleoresin from four directional aspects at each of four positions on the boles of four trees

TREE #	SOURCE OF VARIATION	df	MEAN SQUARE	F
21	Between positions	3	136.521	5.725 *
	Error	12	23.845	
	Between aspects	3	11.611	0.221
	Error	12	52.656	
24	Between positions	3	384.584	38.259 **
	Error	12	10.052	
	Between aspects	3	6.023	0.058
	Error	12	104.692	
25	Between positions	3	239.484	8.411 **
	Error	12	28.473	
	Between aspects	3	40.578	0.519
	Error	12	78.199	
26	Between positions	3	5.953	0.892
	Error	12	6.677	
	Between aspects	3	2.006	0.262
	Error	12	7.664	

* Variance due to differences in amount of flow between positions is significant at the .05 probability level.

** Variance is significant at the .01 probability level.

Table 9b— T tests of differences in mean amount of flow at the ten-inch top and breast height positions

Tree No.	MEAN FLOW AND STANDARD ERROR 10-inch top (grams/24 hrs.)	Breast height (grams/24 hrs.)	df	t
21	4.145 ± 0.774	17.545 ± 3.354	6	3.893 **
24	4.292 ± 1.134	24.078 ± 2.614	6	6.943 **
25	8.235 ± 0.570	22.642 ± 2.864	6	4.933 **
26	4.880 ± 0.879	7.025 ± 0.911	6	1.694

**Difference in the mean amounts of flow is significant at the .01 probability level.

Figure 11. -- Oleoresin exudation during 24 hours from wounds along the boles of four trees.

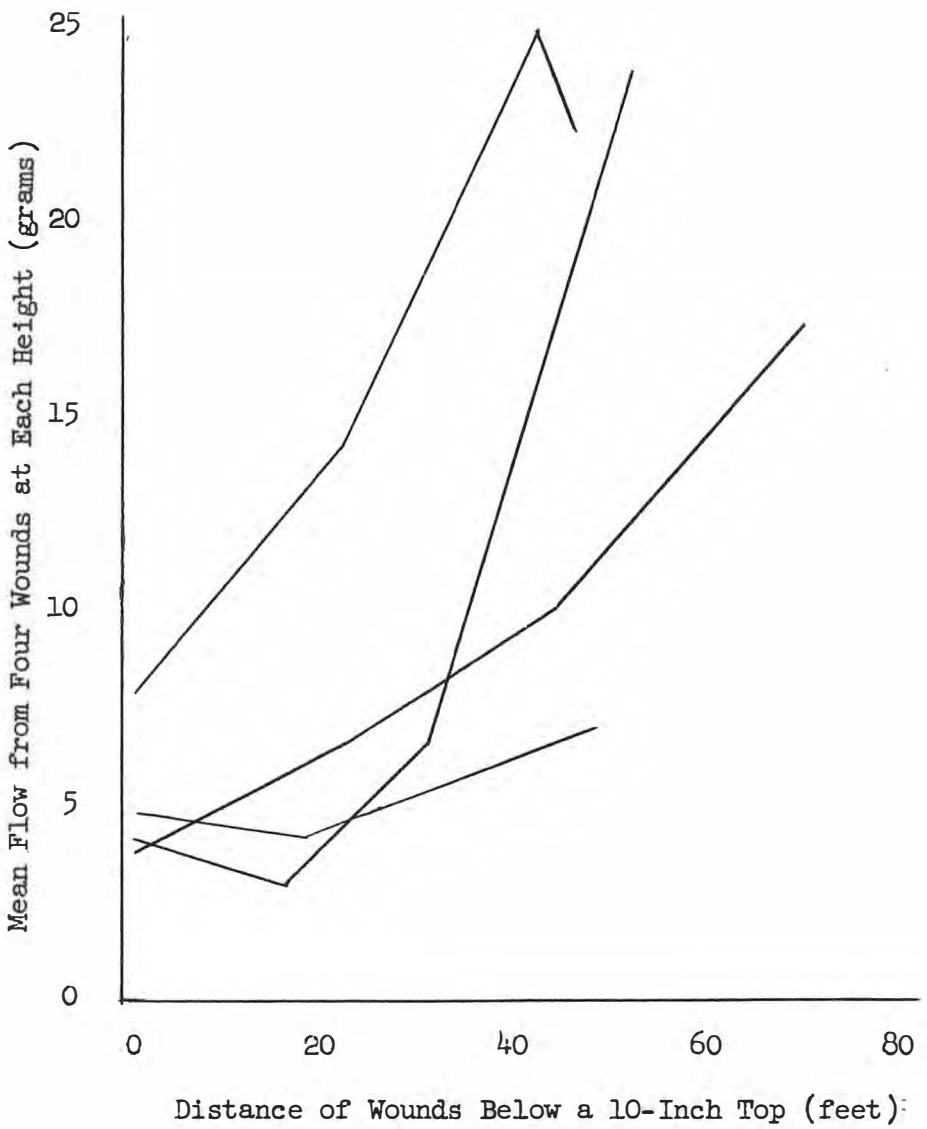

Figure 12. -- Mean 24-hour oleoresin exudation from trees on two plots tapped in June and August 1953.

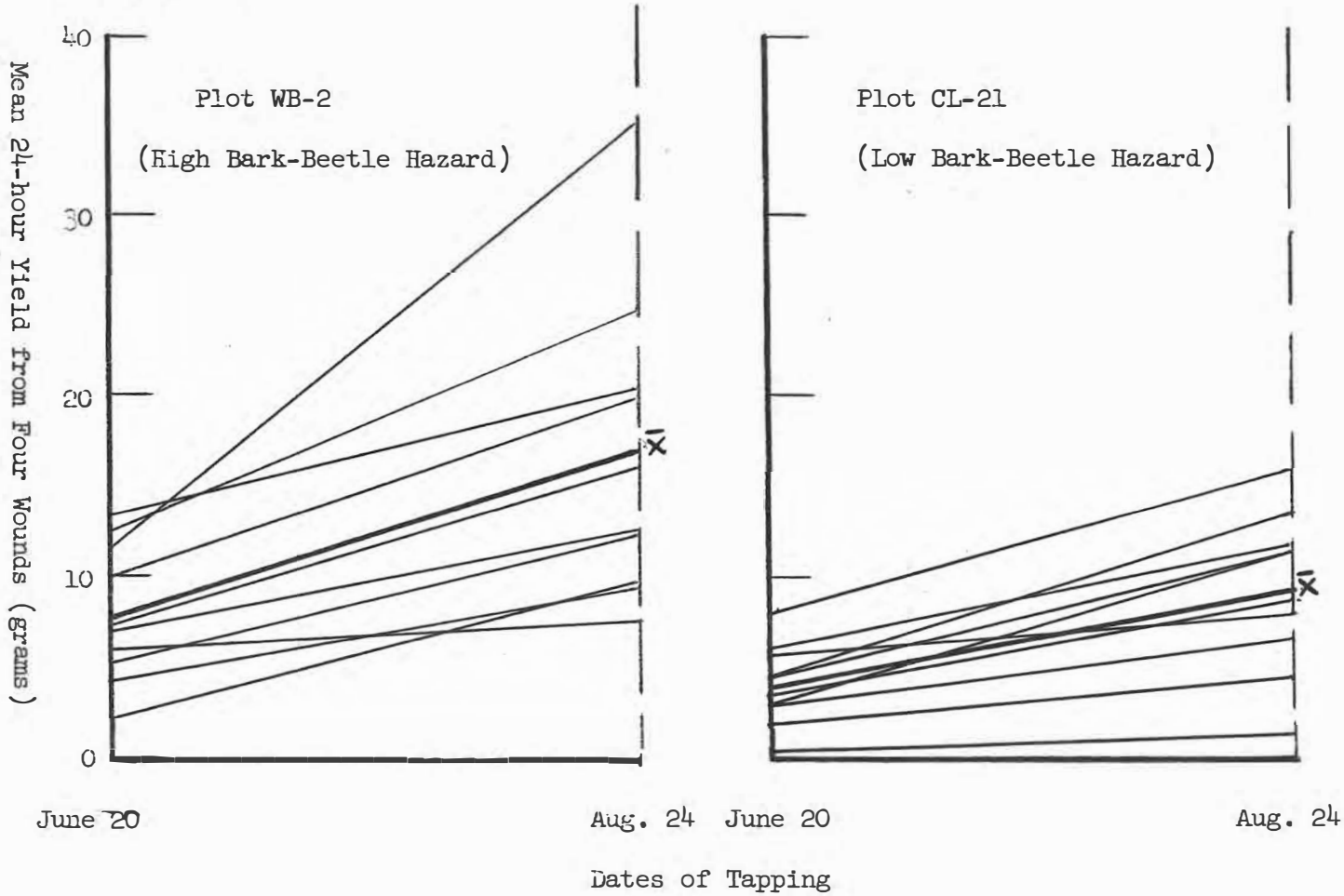

Table 10.-- T tests of differences in mean amount of oleoresin flow per plot of ten trees in June and August

PLOT NO.	MEAN FLOW AND STANDARD ERROR JUNE 10, 1953 (grams/ 24 hrs.)	AUGUST 24, 1953 (grams/ 24 hrs.)	df	t
WB-2	7.954 ± 1.156	17.182 ± 2.784	18	3.062 **
CL-21	3.768 ± 0.705	9.087 ± 1.443	18	3.312 **

** Difference between the mean amounts of flow is significant at the .01 probability level.

One might speculate as to the basis for a decreased flow of oleoresin in the tops of trees. Münch (1921) presented a very logical explanation of the mechanism of resin excretion. He proposed that the osmotic relations of the parenchymatous cells of the epithelium partially govern the excretion of oleoresin from the severed duct. These cells can exert pressure upon the oleoresin contained in the resin canal by virtue of their high osmotic concentration. The pressure exerted would be dependent upon the diffusion pressure deficit between the epithelial cells and the surrounding water-filled tracheids. In these tracheids the moisture tension would be higher in the tree top and lower at the base. Thus, the diffusion pressure deficit would be greater in the tops, and exudation pressure would be less. If the deficit were great enough the top of the tree would not produce any oleoresin. In this way it would resemble slash. There would be no oleoresin produced as far down the stem as the diffusion pressure deficit was limiting. One might speculate that this could be the factor governing the progression of Ips attacks down the stem. The greater the deficit, the farther down the killing would go.

This very brief explanation of the mechanics of exudation also could suggest a basis for explaining the effect of drought on exudation. During drought, the available soil moisture would be reduced, and the aerial portions of the tree would be subjected to high temperatures and low humidity. These two factors probably would result in an increase in the diffusion pressure deficit between the plant and its aerial and soil environments. The resulting extremely high moisture tension would reduce the intake of water by the epithelial cells. It is possible that some water could be taken in by these cells before soil moisture reached the wilting point. However, when soil moisture fell below the wilting point, the moisture content of the tree actually would begin to drop (Satoo and Namura, 1953). Without water there would be no increase in turgor, and there would be no pressure exerted upon the oleoresin to cause it to exude from a severed duct.

FLOW RATE IN SUSCEPTIBILITY TO THE MOUNTAIN PINE BEETLE

The mountain pine beetle is second in importance only to the western pine beetle as an enemy of ponderosa pine in California. It usually attacks valuable mature trees, but in the past three or four decades it has been found in epidemic proportions in young pine stands.

The factors governing the success of attacks by this insect on ponderosa pine have not been investigated; however, some work has been done on the susceptibility of sugar pine, P. lambertiana Dougl. The latter work was summarized by Struble[11]. Struble found that crown characters can not be used in estimating the susceptibility of mature trees. He also found by forcing the beetles to attack trees of different growth rates that "all slow growing trees were overcome and completely killed within a short period, while varying degrees of resistance were shown in the medium and fast growing groups." Clements (1953) studied an outbreak of this insect in young second-growth sugar and ponderosa pines. He found that the occurrence of insect attack was correlated with two stand characteristics: (1) stocking (number of trees in relation to the average diameter of the stand), and (2) crown class (based on the proportion of each dominance class in the stand). Thus, the most severe outbreaks were the result of successful attacks on the intermediate and suppressed trees in the densest young stands.

This work of Struble and Clements merely has indicated which ponderosa pines should be most susceptible to the mountain pine beetle; the question of why these particular trees should be more susceptible remains unanswered. As mentioned in the introduction, Struble proposed that the amount of oleoresin exuding from a tree determines its ability to resist attacks of this beetle. This concept would concur with the general hypothesis that the potential oleoresin flow of the host is the first critical factor determining the success of bark-beetle attacks. If this postulate were correct, one might expect less oleoresin exudation both from slow-growing mature trees and from the slow-growing intermediate and suppressed trees in dense young stands.

An investigation was undertaken in 1953 to determine whether the latter postulate could be substantiated. An outbreak of this bark beetle in second-growth ponderosa pine stands provided suitable material for a cursory field study. Many young trees were analyzed to determine the amount of pitch which they had produced in response to attack. These trees were of all dominance classes, and some had succumbed to beetle attack while others had resisted. In these investigations the weight of the pitch tubes was assumed to be an expression of the oleoresin production potential of the tree[12].

Flow from Resistant and Susceptible Trees of the Same Dominance Classes

In the particular mountain pine beetle outbreak which was studied, adjacent trees of similar diameter and of the same dominance class varied considerably in their susceptibility to similar concentrations of attacks. One living tree would be covered with large pitch tubes characteristic of "pitched out" attacks. Its immediate neighbor would be dead but with much smaller pitch tubes. The amount of oleoresin which had exuded from each attack was weighed. From the data it was possible to determine whether resistant trees had actually produced more oleoresin at each attack than had their susceptible neighbors.

11/ G.R. Struble. Summary of investigative and control work on the mountain pine beetle in sugar pine stands of California. Manuscript Report. California Forest and Range Experiment Station. 1945.

12/ It should be noted that this assumption would be valid only if the attack potentials of all bark beetles were equal.

The Experiment

Experimental trees.— The mountain pine beetle outbreak which was studied occurred in a dense, young stand of second-growth ponderosa pine. The infestation started in 1951, and by 1953 it had resulted in the death of a considerable number of trees. This timber was situated in the Joseph Creek drainage, northeast of Alturas, California. One area of heavy loss was located along the road leading to the Joseph Creek trail, T 44 N, R 20 E, Sec. 35. There were many dead trees adjacent to this road; in addition, there were a few trees which had successfully resisted concentrated attacks. These resistant trees and their immediate neighbors which had succumbed were selected for study. An attempt was made to minimize the influence of seasonal variability in resistance; the only trees selected for study were those which had been attacked in the fall of 1953. These trees still contained insect broods. Such trees were identified by the color of the foliage and by the nature of the pitch tubes.

Collection of data.— The area of infestation was visited in June 1954. Study areas were established wherever trees which had successfully resisted concentrated attacks were found. These study areas typically were group kills where several trees had been killed at the same time. Each resistant tree was classified as to its dominance in the stand; that is, as to whether it was dominant, codominant, intermediate, or suppressed. Its circumference at breast height was measured. The pitch tubes were collected and weighed from a circumferential band, six inches above and below breast height, and the attacks within this area were counted. On each study area this procedure was repeated on the dead trees which were comparable to the resistant trees in dominance class and diameter. This gave data for two classes of trees, one resistant and one susceptible, within the four dominance classes.

Analysis of data.— The field data were analyzed by statistical methods. It was determined whether attacks on resistant trees had produced larger pitch tubes than had attacks on the susceptible individuals. The mean weight of oleoresin per attack was determined for each tree. These data were subjected to an analysis of variance in a one-way classification with two classes of unequal size. The statistical test given on page 19 was used.

The Results

Table 11 gives the results of the variance analysis. Note the extremely highly significant difference in the size of pitch tubes between resistant and susceptible trees. This confirms the general field observation that "pitched out" attacks are characterized by abnormally large pitch tubes. Certainly, it is in support of the hypothesis that resistance is dependent upon oleoresin production potential. It was noted in the field that the unsuccessful attacks resulted in little or no gallery construction. Usually there was only a small excavation of the phloem directly beneath the entrance. It would seem logical to suggest that the difference in the size of pitch tubes was either the result of an extremely high oleoresin production potential on the part of the resistant trees or a very much diminished potential on the part of the susceptible trees.

Table 11.— Analysis of the weight of pitch tube per attack on trees of the same dominance classes which were resistant and susceptible to the mountain pine beetle

ANALYSIS OF VARIANCE

SOURCE OF VARIATION	df	MEAN SQUARE	F
Between resistant and susceptible trees	1	28.6594	59.509 ***
Error	36	0.4816	

	n	Mean weight of pitch tube/ attack
Resistant trees:	13	1.96 g.
Susceptible trees:	25	0.13

***Variance due to difference between classes is significant at far less than the .001 probability level.

Flow from Susceptible Trees of Different Dominance Classes

In the stand under investigation trees of all dominance classes had been attacked and killed. The larger dominant and codominant individuals seemed to have produced more oleoresin in response to attack than did trees of the smaller intermediate and suppressed classes. The quantity of oleoresin exuding at each point of attack was weighed to ascertain whether this observation was correct. Investigators in the southern turpentine region have found in general that the larger trees of the stand produce the most oleoresin.

The Experiment

Experimental trees.— The trees used in this phase of the study were the susceptible individuals studied in the preceding investigation.

Collection of data.— Each study area was revisited after the data for the foregoing comparisons had been collected. The procedures described for the preceding investigation were used in examining all of the remaining dead trees in each area. This provided data for dead trees in the four dominance classes.

Analysis of data.— The field data were used to determine for each tree the mean weight of the pitch tube formed at each entrance. As before, these data were subjected to analyses of variance using a one-way classification with classes of unequal size.

The Results

The results of the several variance analyses have been tabulated (table 12). The first variance analyses showed that there was a highly significant difference between dominance classes in the amount of oleoresin at each beetle entrance on dead trees. The significant differences both between dominant and codominant individuals and between codominant and suppressed individuals indicated that there may actually have been only three distinct classes involved: dominant, codominant-intermediate, and suppressed. This would seem logical on the basis of the manner in which the trees were classified in the field. Dominant and suppressed individuals were classified quite readily; however, codominant and intermediate individuals were difficult to separate in this dense young stand. Regardless of this latter problem, the data showed quite conclusively that attacks on dominant trees produced the largest pitch tubes and that attacks on suppressed trees produced the smallest ones. Thus, the postulation that the slower-growing intermediate and suppressed trees produce less oleoresin was substantiated. This of course was based on the original assumption that smaller pitch tubes represent a reduced oleoresin production potential. The significance of this finding lies in the relationship found by Clements. He found the attacks concentrated on suppressed trees during the build up of an epidemic. The reduced oleoresin production from these trees certainly may play an important role in the relatively higher susceptibility of these trees.

INVESTIGATION OF THE CAUSES OF VARIATION IN OLEORESIN FLOW

The preceding investigations do seem to support the original hypothesis that the susceptibility of a tree is related to its oleoresin production potential. Therefore, one next might ask: "What are the factors responsible for the observed tree-to-tree differences in oleoresin production potential?"

To answer this question, one logically first should turn to the extensive literature on research in the naval stores industry. Such investigation has been continuing for many years both in this country and in Europe. Two of the first fundamental studies of the scientific principles underlying the exudation of oleoresin were conducted by Münch (1921) and Ivanov (1930). They concentrated on the relation between oleoresin exudation and both the longitudinal resin ducts[13/] and the radial rate of growth. The work in this country up to 1935 has been compiled by the U.S. Forest Service and others (1935) in "A Naval Stores Handbook."

The most recent article pertaining to individual tree differences in oleoresin production potential was one by Schopmeyer, Mergen, and Evans (1954). Their article briefly outlined the factors "which have been measured or suggested for possible correlation with the capacity of the tree to yield oleoresin"; morphological, anatomical, physical, and chemical factors were included. None of the early work had resulted in the determination of the fundamental bases of oleoresin exudation; however, these three men finally seem to have derived a satisfactory explanation for differences in oleoresin flow from tree-to-tree, in fact from wound-to-wound.

13/ Longitudinal (vertical) resin ducts are those which follow a course in the xylem parallel to the pith.

Table 12.—Analyses of the weight of pitch tube per attack on trees of different dominance classes killed by the mountain pine beetle

ANALYSES OF VARIANCE

SOURCE OF VARIATION	df	MEAN SQUARE	F
Between dominant, codominant, intermediate and suppressed tree classes	3	0.3552	8.018 **
Error	45	0.0443	
Between dominant and codominant tree classes	1	0.7107	10.801 **
Error	25	0.0658	
Between codominant, intermediate and suppressed tree classes	2	0.0844	2.851
Error	43	0.0296	
Between codominant and intermediate tree classes	1	0.0354	1.000
Error	36	0.0354	
Between codominant and suppressed tree classes	1	0.1641	5.311 *
Error	30	0.0309	
Between intermediate and suppressed tree classes	1	0.0531	3.052
Error	20	0.0174	

DOMINANCE CLASS	n	MEAN WEIGHT OF PITCH TUBE/ATTACK
Dominant	3	0.687 g.
Codominant	24	0.170
Intermediate	14	0.107
Suppressed	8	0.005

* Variance due to differences between classes is significant at the .05 probability level.

** Variance is significant at the .01 probability level.

They were able to show experimentally that the flow of oleoresin during the first 24 hours after wounding was in large part the product of three independent factors. These factors were: (1) the reciprocal of the viscosity of oleoresin, (2) the number of transverse resin ducts[14] which are exposed in wounding, and (3) the capacity of the same resin ducts. These are three of the four variables in Poiseulle's law for the movement of viscous liquids through capillaries. A fourth variable, the pressure on the liquid in the capillaries, probably also plays a significant role in the determination of oleoresin exudation. No one, including Schopmeyer and his colleagues, has been able to measure such pressure accurately (MacDougal, 1925 and 1925a; Arbuzov, 1925).

The excellent work of Schopmeyer and his associates provided for the first time a means of explaining wound-to-wound variability in flow. With their study as a foundation the decision was made to conduct two studies. First, it was planned to test the applicability of Poisseulle's law to the exudation of oleoresin from ponderosa pine. Second, it was to be determined whether variations in viscosity, size of ducts, or number of transverse resin ducts might account for the variations in oleoresin production which seem to be associated with bark-beetle susceptibility. The collections of data for both investigations were carried out concurrently.

THE APPLICABILITY OF POISEULLE'S LAW TO OLEORESIN EXUDATION

Poiseulle's original law was modified by Schopmeyer and his colleagues in applying its principles to oleoresin exudation. The equation as modified by them was:

$$Y = \frac{KPN\overline{(ab)^2}}{H} \qquad (1).$$

In this equation Y was the yield of oleoresin during the first 24 hours after wounding; K was a constant; P was the pressure of exudation at the point of discharge from the resin ducts; N was the number of transverse resin ducts per unit area of tangential wound surface; $\overline{(ab)^2}$ was the mean measure of the capacity of elliptical transverse resin ducts whose major and minor semi-axes were a and b; and H was the viscosity of the oleoresin.

Schopmeyer and his coworkers were able to demonstrate that each of the three factors, oleoresin viscosity, number of resin ducts, and capacity of resin ducts, was significantly correlated with variations in flow rate. In a multiple correlation analysis they found that these three variables "accounted for 83 percent of the variation in flow rate between trees." In their investigation on slash pine, P. elliottii Engelm. var. elliottii, they found that they could not measure accurately the effect of pressure on yield.

14/ Transverse (horizontal) resin ducts are those which follow a radial course in the xylem and phloem rays. They are interconnected with the longitudinal system of resin ducts in the xylem.

Despite the soundness of their results, it is conceivable that each of the three factors would not be as important with respect to a different species growing in a different environment. The particular trees which they studied were growing in the hot, humid summer climate of the central part of northern Florida. It was a low site where the water table was at the level of the ground surface. In direct contrast to such conditions, the ponderosa pine stands in the West typically exist under arid, semi-drought conditions in summer. This fact alone might be expected to affect the importance of these three variables in determining yield.

In recognition of these differences in growing conditions several investigations were carried out to determine for ponderosa pine the applicability of Poiseulle's law, as modified by Schopmeyer, Mergen, and Evans. These investigations involved trees growing both in different areas and at different seasons. They were conducted in conjunction with the studies of rate of flow of oleoresin discussed in preceding sections.

The Experiment

Experimental Trees

The trees used in this investigation were located on the plots described in table 3. The trees varied from one extreme to the other with respect to age, vigor, and current health.

Collection of Data

Yield determinations.—Yield measurements were a part of the oleoresin flow rate studies described on pages 9 and 43. Only the yield during the first 24 hours after tapping was used.

Viscosity measurements.— The oleoresin collected during this interval was analyzed for viscosity in the laboratory. The vials containing the exuded oleoresin were stoppered in the field. Then after all of the yield determinations had been completed, the vials were taken into the laboratory. Each oleoresin sample which did not show any signs of crystallization was subjected to a viscosity measurement. Viscosity was measured by the bubble-rise technique; the time required for an air bubble to rise through the liquid in a vertically positioned tube was an expression of the liquid's viscosity. The standard Gardner viscometer tube is commonly used for such measurements; the time of bubble rise in this tube equals the viscosity of the liquid in Stokes. The standard Gardner tube had too large a capacity for the purposes of these investigations; hence, a large series of dental procaine vials of approximately 3 cc. capacity were adapted for use. Each of these vials was calibrated against the standard Gardner tube. The standard tube was not calibrated for accuracy; therefore, the expressions of viscosity derived from the small viscometer tubes were merely relative. All viscosity determinations were made in a water bath at 30.0°C. The variation in bath temperature, as determined with a Beckman thermometer, was not more than $\pm$ 0.005° C. For each oleoresin sample the bubble rise was timed repeatedly until four observations, agreeing within one to two percent, were obtained.

Resin duct measurements.— Measurements of the transverse resin ducts were made from histological specimens which were prepared from the wood exposed by tapping. After yield measurements had been completed, the tapping device was removed. An arch punch (figure 4), $1\frac{1}{4}$ inches in diameter, was used to remove a disc of wood from the area exposed by the tapping. The wound number was written on each disc, and the discs were placed in a jar containing 50 percent ethyl alcohol. The discs thus were stored until the end of the field season when they were sectioned in the laboratory. Transverse sections and tangential cambial sections, 20 microns in thickness, were cut with a sliding microtome. The best sections from each block were mounted on a microscope slide by means of rubber bands.

These slides were moved through a series of solutions to prepare the sections for study. The slides were passed through acetone-water (1:1) to acetone and returned through the acetone-water to water. This procedure, involving five minutes in each solution, removed the excess oleoresin from the sections. Then the sections were stained for thirty minutes in an aqueous solution of one percent Safranine O, rinsed in water, dehydrated through a series of ethyl alcohol solutions, and counterstained in $\frac{1}{2}$ percent fast green in absolute ethyl alcohol for one minute. Finally, they were rinsed in absolute alcohol and mounted directly in diaphane.

The number of transverse resin ducts per souare millimeter was determined from the tangential sections. All of the resin ducts were counted under a magnification of 60x. The area of each section was determined concurrently by means of the mechanical stage. These values were used to calculate the number of ducts per mm^2.

Twenty transverse ducts were systematically selected and measured on each section. Measurements were made by means of an ocular micrometer at a magnification of 264x. In a diagonal transect across the slide from one corner to the opposite corner the first twenty measureable (intact) ducts were scaled. These ducts were elliptical in contrast to the normally circular longitudinal ducts. Both the major axes (2a) and the minor axes (2b) of the elliptical ducts were measured. In all cases measurement was made to the outside of the single circle of epithelial cells. Following the modification of Poiseulle's law, flow through each duct was assumed to be proportional to $(ab)^2$. Hence, this value was computed for each measured duct. From twenty such values the mean, $\overline{(ab)^2}$ was calculated for each slide.

Analysis of Data

The data were subjected to a treatment similar to the one used by Schopmeyer and his colleagues. First it was necessary to determine the significance of each variable in the modified Poiseulle's law. The pressure factor, P, was not studied; hence, it could not be incorporated in the analyses. Following Schopmeyer, it was assumed "that each variable had an unknown power. . . ." Thus, the original equation was rewritten:

$$Y = K\,(1/H)^{b_1}\,N^{b_2}\,\overline{(ab)^2}^{\,b_3} \qquad (2).$$

When this equation was transformed to logarithms, it gave the familiar regression equation:

$$\log Y = \log K + b_1 \log (1/H) + b_2 \log N + b_3 \log \overline{(ab)^2} \qquad (3).$$

The variables of this equation were analyzed to determine the significance of values of b_1, b_2, and b_3. Later, further analyses were conducted with those factors which were shown to be correlated with yield.

The Results

General Applicability

The general applicability of the modified law to ponderosa pine oleoresin yield was investigated first. The data obtained from wounds on mature and overmature trees growing on plots 1-3 were used. For the purpose of this study, 34 wounds for which accurate viscosity measurements were available were used. In some cases two or three of these wounds were on the same tree. The partial regression coefficients in formula (3) were calculated. These coefficients, their standard errors, and significance, as determined by t tests, are given in table 13. Only the coefficient of partial regression of yield on viscosity was significantly different from zero. Exactly the same results were obtained when only one wound on each of 27 trees was used in the regression analysis. These results indicated, under the conditions of this study, that yield was a function of viscosity alone. Contrary to Schopmeyer's finding, the results indicated that yield was not influenced either by changes in the capacity or by changes in the number of resin ducts. However, it must be explained at this point that the selection of wounds for study may have introduced undue bias; the only wounds selected were those which gave a sample of oleoresin suitable for viscosity measurements. As a result of this selection, wounds producing less than three grams of oleoresin in 24 hours were excluded for lack of sufficient material for viscosity measurement; similarly, wounds producing in excess of ten or so grams usually were eliminated because of excessive crystallization of the oleoresin.

An attempt was made to eliminate this source of bias in another analysis. A large series of 128 wounds on 52 trees, including the 34 wounds used in the preceding analysis, was analyzed to determine the regression of yield on capacity and number of ducts. Wounds yielding both small and large amounts of oleoresin were adequately represented in this analysis. Viscosity determinations had not been completed for the oleoresin samples obtained from all of these wounds; therefore, viscosity was eliminated from the analysis.

A modification of formula (3),

$$\log Y = \log K + b_2 \log N + b_3 \log \overline{(ab)^2} \qquad (4),$$

was used to evaluate the significance of number and capacity of resin ducts in this larger series. The partial regression coefficients, their standard errors, and their significance, as determined by t tests, are given in table 13. The coefficients of partial regression both of yield on number of resin ducts and of yield on capacity of resin ducts were significantly different from zero. This indicated that yield was a positive function of number of resin ducts but a negative function of capacity of resin ducts. Therefore, yield would increase with an increase in number of ducts, or a decrease in capacity of ducts. The latter result is in direct conflict with Schopmeyer's positive correlation between yield and capacity of ducts which one logically would expect to find.

Table 13.-- Partial regression coefficients and their standard errors for $\text{Log } Y = \log K + b_1 \log (1/H) + b_2 \log N + b_3 \log \overline{(ab)^2}$ 1/

Study	n	b_1' 2/	b_2' 3/	b_3' 4/
Plots 1-3	34	$+.409 \pm .041$**	$+.063 \pm .240$	$+.181 \pm .191$
Plots 1-3	128		$+.041 \pm .008$**	$-.072 \pm .008$**
Plots WB-2 + CL21 June	33		$+.679 \pm .132$**	$-.102 \pm .132$
Plots WB-2 + CL 21 Aug.	33		$+.735 \pm .123$**	$-.111 \pm .123$
Plots WB-2 + CL21 June	17	$+.839 \pm .224$** 5/		
Plots WB-2 + CL21 Aug.	12	$+.154 \pm .596$ 5/		

1/ Y = yield of oleoresin in grams during the first 24 hours after tapping; 1/H = reciprocal of viscosity in Stokes; N = no. of resin ducts/mm^2; and ab = semi-axes of elliptical resin ducts.

2/ $b_1 = b_1'_{\text{logY log (1/H)} \cdot \text{log N log } \overline{(ab)^2}}$

3/ $b_2 = b_2'_{\text{logY logN} \cdot \text{log (1/H) log } \overline{(ab)^2}}$

4/ $b_3 = b_3'_{\text{logY log } \overline{(ab)^2} \cdot \text{log (1/H) log N}}$

5/ Regression coefficient, not partial regression coefficient.

** Deviation of the statistic from zero is significant at the .01 probability level.

Returning now to Schopmeyer's procedure of analysis, the actual values of the variables shown above to influence yield were used in regression analyses. The following regression equations were computed:

$$Y = a + b\,(1/H) \qquad (5),$$

for the original 34 wounds, and

$$Y = a + b\,(N \overline{(ab)^2}) \qquad (6),$$

for the large series of 128 wounds. The solution to equation (5) was $Y = 4.07 + 16.95\,(1/H)$; the coefficient of correlation was 0.47, which was highly significantly different from zero; the coefficient of determination was 0.22. Thus, 22 percent of the variation in yield was associated with positive variation in the reciprocal of viscosity. This is in good agreement

with Schopmeyer's results. The solution to equation (6) was $Y = 5.31 + 4.02 (N (ab)^2)$; the coefficient of correlation was + 0.10, which was not significantly different from zero; the coefficient of determination was + 0.01. Thus, only an inconsequential one percent of the variation in yield was associated with positive variation in the product of number of resin ducts and capacity of resin ducts.

The foregoing calculations lead one to a conclusion in agreement with Schopmeyer and the others. For relatively old ponderosa pines growing under the conditions of this study, oleoresin flow during the first 24 hours after tapping was significantly determined by viscosity of the exuding gum. The number and capacity of the resin ducts exposed by wounding had little influence in determining yield. This latter point is in direct contradiction to the findings with respect to young slash pine.

It is very difficult to develop a logical explanation for this disagreement in results. The experiments were conducted in essentially the same manner; yet, opposing results were obtained. Many conditions could have produced these results. Some of these conditions may have been: the difference in tree species, the difference in the ages of trees under study, the difference in environment, the unknown but probably considerable difference in oleoresin exudation pressure, the fact that all ducts were assumed to be functioning in conducting oleoresin, the fact that capacity evaluation was based on measurements of the ducts rather than the actual canal opening. Of course some of these items are interrelated. Münch demonstrated that exudation pressure was dependent upon water stresses within the stem. The opening of the normally closed transverse canal must be dependent upon the exudation pressure. In connection with this latter point, Erickson (1938) found that transverse resin canals were somewhat variable in their opening under pressure. He speculated that this might have been due to tyloses or resin plugs in the canals. If such obstructions were present, the number and capacity of truly functional ducts would be less than the maximal values used in the computations.

Seasonal Differences in Applicability

Investigations also were carried out to determine the applicability of the modified law to ponderosa pine oleoresin yield in other localities and seasons. The trees on plots WB-2 and CL-21 were used for a study of the seasonal variability in oleoresin exudation. This study was discussed in a preceding section. The wounds made for that yield study were used to evaluate the determination of variation in yield by the factors of Poiseulle's law. Thirty-three wound positions, tapped both in June and August 1953, provided the data for these analyses. Data were obtained on the number and capacity of ducts exposed on all 33 wounds at both tappings. Viscosity determinations only could be made on the oleoresin exuding from 17 of the wounds, in June and from 12 of the wounds in August. A modification of equation (3), $\log Y = \log K + b_1 \log (1/H)$, was used to determine the significance of b_1 for both the June and August tappings. Equation(4), $\log Y = \log K + b_2 \log N + b_3 \log (ab)^2$, was used to determine the significance of b_2 and b_3 at both tappings. These regression coefficients and partial regression coefficients, their standard errors, and their significance are given in table 13.

Only three statistics showed a significant deviation from the null hypothesis. They were the coefficient of regression of yield on viscosity in June and the partial coefficient of regression of yield on number of ducts in June and August. Thus, in June, variation in yield was a function both of viscosity of oleoresin and of number of resin ducts; whereas, in August only number of resin ducts seemed to influence yield. The change in the significance of viscosity from June to August may have been due to the small number of wounds studied at the later date. The calculations also indicated that the capacity of the resin ducts exposed by tapping in June and in August was not a significant factor in determining variations in yield of oleoresin. There was not a statistically significant difference between the June and August values of b_1, of b_2, and of b_3. Thus, there was no evidence to indicate that there were changes during the season in the significance of viscosity, or number of ducts, or capacity of ducts in determining oleoresin yield.

The regression, $Y = a + b\ (N/H)$, was computed, using the actual values of the factors shown to be significant in determining yield. The solution to this regression using the June data for 17 trees was $Y = 4.65 + 48.04(N/H)$; the coefficient of correlation was + 0.44, which was significantly different from zero; the coefficient of determination was + 0.19. Thus, 19 percent of the variation in yield was associated with positive variation in the number of resin ducts divided by the viscosity of the oleoresin. The solution to the same equation using the August data was $Y = 10.72 + 21.58\ (N/H)$; the coefficient of correlation was + 0.10, which was not significantly different from zero.

VARIATION IN OLEORESIN VISCOSITY

From the foregoing investigations it was obvious that oleoresin viscosity was a significant factor in determining oleoresin yield during the first 24 hours after wounding. If we apply this knowledge to the problem of the susceptibility of pines to bark beetles, it is conceivable that a basic understanding of the nature and cause of variability in viscosity might be important in the analysis of the question of resistance. The question of variability in resistance might not seem so perplexing if we knew more about the variability in viscosity. Of particular interest would be (1) changes day by day after wounding, (2) changes from season to season during the year, (3) changes from one position to another on the bole of each tree, (4) changes in the temperature, and (5) changes in the composition of the oleoresin.

Viscosity Changes after Tapping

The earlier discussion of flow rate brought out the fact that oleoresin flow diminished rapidly in the first few days after wounding. It also has been established that flow rate is a negative function of oleoresin viscosity. One might hypothesize then that this reduced flow is the result of a day-to-day increase in the viscosity of the oleoresin. Schopmeyer[15/] investigated the validity of this hypothesis for slash pines tapped in May

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15/ C.S. Schopmeyer. Report of physiological studies made in 1950. Manuscript Report. Lake City Research Center, Southeastern Forest Experiment Station. 1950.

and June. He found the viscosity of oleoresin samples collected on the second day in general to be significantly higher than those collected on the first day. However, viscosities of third day samples were not significantly different from those collected on the first day. He was not able to compare viscosities from more than three days.

The Experiment

The validity of this hypothesis with respect to ponderosa pine was investigated during the 1953 field season. The study was made in conjunction with the flow rate experiments on plots 1-3. The daily increments of oleoresin were collected individually and were measured gravimetrically as described on page 18. It should be noted that all increments of oleoresin subsequent to the one collected on the first day had to flow through the collection device over gum containing resin acid crystals. At the end of each field day the oleoresin samples were subjected to viscosity measurements as described on page 55. Viscosity was measured only on those oleoresin samples which did not show any signs of crystallization. The mean viscosities of oleoresin samples collected from the same wounds on different days were compared by means of t tests.

The Results

The results of these t tests are given in table 14. The t values obtained do not provide any reason to suspect that there is any change in oleoresin viscosity during the first five days after tapping. On the basis of fairly large samples, there does not seem to be any evidence to indicate that there is a significant difference in viscosities on successive days; however, larger samples for comparisons over a two or three day interval might substantiate the hypothesis. The sample sizes on which these t tests were based were very meager in comparing days which were two or three days apart.

Viscosity Changes during the Year

The seasonal flow rate study described on page 43 showed a higher rate of oleoresin exudation in the summer than in the spring. Experience in other regions (U.S. Forest Service et al., 1935, p. 81) also has shown that midsummer yields are higher than those obtained in spring and fall. Is this seasonal variability in flow associated with seasonal differences in viscosity? Schopmeyer investigated this question in 1950. His data for slash pine indicated that there was a decrease in viscosity during May. There was little subsequent change in viscosity during the next three or four months. He concluded:

> "The decrease in viscosity during the month of May is a factor, in addition to increasing temperature, which accounts for the more rapid flow of oleoresin during the summer than during the spring. This change in viscosity also indicates that oleoresin from ducts formed in the current year may differ in viscosity. . . from oleoresin exuded from older tissues."

Mergen, Hoekstra and Echols (1955), without supporting data, state: "During the active growing season there is a pronounced change in viscosity, the highest value occurring at the beginning of the season and then decreasing rapidly. It appears to stabilize during the month of June."

The Experiment

Two investigations were conducted to determine for ponderosa pine the seasonal variation in oleoresin viscosity. The first of these studies was undertaken in conjunction with the determinations of oleoresin flow rate on plots WB-2 and CL-21. A comparison was made of the mean viscosities of the oleoresin samples which were collected. The samples were procured both in June and again in August from twelve wounds. These wounds were on the same trees and at the same aspects. Tapping and viscosity determination procedures are described on pages 43 and 55.

The second study was more comprehensive, and it extended over a period of nearly two years. A series of vigorous young trees was tapped at the Institute of Forest Genetics, Placerville, California. The viscosity of oleoresin from five trees was followed for two years, and the viscosity from nine trees was followed for one season. Tapping was done intermittently at six to ten-week intervals. The tapping procedure used was to bore a hole at breast height about two inches into the wood with an $1\frac{1}{2}$ inch wood bit. This procedure was required to obtain in a short time large non-crystalline oleoresin samples for viscosity determinations. Viscosity in this second study was determined as before.

The Results

The first comparison of mean viscosities of oleoresin collected both in June and in August was made by means of a t test. This test indicated that the difference between the mean viscosities was not sufficient to make suspect the null hypothesis. The mean viscosities in Stokes were: for June, 8.903 ± 0.817, and for August, 8.328 ± 1.028.

Viscosities from the second study are given in tables 15 and 16. Analyses of variance (tables 15 and 16) indicate that the variance due to differences in viscosity of oleoresin on different dates is not significant at the .05 probability level. Neither of these studies has provided any evidence in support of the hypothesis that oleoresin viscosity changes within the tree from season to season during the year.

Viscosity Changes with Position on the Bole

Two questions are of concern under this heading. (1) Does the viscosity of oleoresin vary from one directional aspect to another at any one level on the bole; and (2) does the viscosity of oleoresin vary from the top to the bottom of the tree? The study reported in table 9 indicated that there was no significant effect of aspect on flow rate; hence, we might expect that there would be no effect of aspect on viscosity. Similarly, table 9 presented evidence that the rate of oleoresin exudation decreased from the bottom to the top of the tree. From this one might postulate that the viscosity of the oleoresin would increase from the bottom to the top of the tree.

Table 14.— Mean viscosities of oleoresin collected from the same wounds on different days after wounding

Days Compared (1) (2)	No. of wounds	Mean (1) Stokes	Mean (2) Stokes	t 1/
1 and 2	19	6.65 ± 0.73	7.00 ± 0.81	0.319
1 and 3	10	7.05 ± 1.02	7.87 ± 1.27	0.499
1 and 4	2	7.32 ± 1.48	7.23 ± 1.33	0.045
2 and 3	28	6.03 ± 0.53	6.40 ± 0.62	0.458
2 and 4	16	5.69 ± 0.73	6.68 ± 0.89	0.862
2 and 5	2	3.97 ± 0.94	5.83 ± 2.15	0.789
3 and 4	15	5.48 ± 0.53	6.01 ± 0.58	0.676
3 and 5	2	4.76 ± 0.34	6.91 ± 1.08	1.901
4 and 5	3	5.00 ± 0.73	5.83 ± 1.24	0.573

1/ None of the t values show a probability of occurrence low enough to make suspect the null hypothesis that both means are random samples from oleoresin of the same viscosity.

Table 15.—Viscosities of oleoresin collected from bore holes on five trees during two years - Institute of Forest Genetics, Placerville, California

Date of Collection	Tree Number				
	5	6	8	16	17
			Stokes		
4/16/53	4.170	5.928	6.336	4.662	5.022
5/18/53	4.148	4.789	9.081	5.253	4.893
8/13/53	4.388	6.732	10.062	4.934	6.500
10/1/53	5.119	5.690	8.123	4.869	6.397
11/4/53	5.251	4.994	8.491	6.715	6.328
2/2/54	4.322	5.814	(9.294)1/	8.956	5.376
4/11/54	6.603	10.606	7.009	(7.275)1/	8.195
4/30/54	4.389	5.912	6.771	4.844	6.684
6/14/54	4.730	9.277	7.443	5.178	6.032
8/11/54	4.629	5.714	8.748	4.815	11.871
9/25/54	5.165	5.740	17.137	5.345	7.203

ANALYSIS OF VARIANCE

Source of Variation	df	SS	MS	F
Between dates	10	41.8998	4.1900	1.173
Within dates between trees	4	105.1779	26.2945	
Error	39	139.2713	3.5711	
Total	53	286.3490		

1/ Statistic missing; value estimated from Snedecor (1946, p.268).

Table 16.— Viscosities of oleoresin collected from bore holes on nine trees during one season - Institute of Forest Genetics, Placerville, California

Date of Collection	Tree Number 5	6	8	16	17	18	20	21	22
					Stokes				
4/11/54	6.603	10.606	7.009	(8.338)1/	8.195	11.014	24.219	5.720	7.510
4/30/54	4.389	5.912	6.771	4.844	6.684	4.951	5.004	5.634	6.873
6/14/54	4.730	9.277	7.443	5.178	6.032	7.433	7.387	5.906	5.871
8/11/54	4.629	5.714	8.748	4.815	11.871	7.298	4.669	7.143	6.168
9/25/54	5.165	5.740	17.137	5.345	7.203	7.356	5.516	7.029	6.448

ANALYSIS OF VARIANCE

Source of variation	df	SS	MS	F
Between dates	4	92.4015	23.1004	2.092
Within dates, between trees	8	91.3434	11.4179	
Error	31	342.3125	11.0423	
Total	43	526.0574		

1/ Statistic missing; value estimated from Snedecor (1946, p.268).

The Experiment

Originally the flow rate study described on page 41 was designed to provide the viscosity data necessary to answer the questions above. However, only a few of the oleoresin samples which were obtained were suitable for viscosity determinations. Nevertheless, the data on viscosity derived from the 1953 flow rate experiments, plots 1-3, can be brought to bear on the problem of variation due to aspect. These viscosity data were obtained from oleoresin samples collected at breast height from four aspects: north, south, east, and west. The oleoresin samples were collected during the first five days after tapping. Each viscosity value used in this particular study represented the mean of all viscosity measurements made of the oleoresin exuding from a single wound. The mean viscosities for different aspects were compared through "t" tests.

During the month of September both in 1952 and 1953, an attempt was made to determine the variation in viscosity from the top to the bottom of the tree. Vigorous young trees growing at the Institute of Forest Genetics

were tapped in this work. Tapping in 1953 was done with the punch shown in figure 4, but in 1952 the trees were tapped with bore holes, one to two inches deep, made with an $1\frac{1}{2}$ inch wood bit. In 1952 the trees were tapped at a ten-inch top, mid-bole, and breast height. Whereas, in 1953, the tapping was done at four positions: ten-inch top, twenty feet and forty feet below the ten-inch top, and breast height. Viscosities in this study and the preceding study were determined by the bubble-rise method described earlier.

The Results

The results of the study of variation in viscosity at different aspects are given in table 17. T tests did not indicate any differences between directionalaspects in viscosity of oleoresin collected at breast height. The inconsistencies in mean viscosity values given for each side from one comparison to another were due to differences in trees which were compared.

The 1952 and 1953 data pertaining to the variation in viscosity from the top to the bottom of the tree did not lend itself to statistical analysis. This was due to the difficulty experienced in obtaining from each tap an oleoresin sample suitable for viscosity measurement. Nevertheless, the available data are presented in graphical form in figure 13. A general downward trend in viscosity from the top of each tree to the base is indicated.

Viscosity-Temperature Relationships

It was necessary during the course of the investigations to measure some viscosities under field conditions. These viscosities at field temperatures had to be converted to viscosities at 30°C. for the preceding analyses. For this reason a study of the relationship of viscosity to temperature was necessary.

It has been known for some time that pine oleoresin viscosity is a function of temperature. Previous work all pertains to oleoresin of slash pine and longleaf pine, Pinus palustris Mill. Smith (1936) and Runckel and Knapp (1946) showed by means of graphs the relationship of viscosity to temperature. Schopmeyer in a personal communication stated that this relationship was linear in the 25 to 35°C. range when logarithmic values both of viscosity and of temperature were plotted. He also emphasized that at higher temperatures there was a convergence of the lines for samples of high and low viscosity. This obviated the possibility of drawing general mathematical expression for the viscosity-temperature relation.

The Experiment

Some of the oleoresin samples used in the 1954 study of seasonal variation in viscosity were analyzed for their viscosities at temperatures higher and lower than the 30°C. temperature used throughout the study. Ultimately viscosity measurements for each oleoresin sample were obtained at 22.5, 30.0, and 37.5 degrees centigrade. All temperatures were determined with a mercury thermometer calibrated to tenths of degrees. Six of the samples collected in August 1954 and four of the samples collected in September 1954 were analyzed at these temperatures.

Table 17.— Mean[1/] viscosities of oleoresin collected from different sides of trees

Comparing (1)	(2)	n	Sides (1) Stokes	(2) Stokes	t[2/]
North	West	20	6.114 ± 0.648	5.945 ± 0.598	.192
North	South	18	6.148 ± 0.477	5.975 ± 0.556	.237
North	East	25	7.389 ± 0.631	7.920 ± 0.855	.500
West	South	16	6.885 ± 1.038	7.346 ± 1.270	.281
West	East	18	7.686 ± 0.988	7.829 ± 0.809	.112
South	East	18	8.198 ± 1.107	8.175 ± 0.940	.016

1/ Means were computed from any measurements of viscosity from the first through the fifth days of flow.

2/ None of the t values show a probability of occurrence low enough to make suspect the null hypothesis that both means are random samples from oleoresin of the same viscosity.

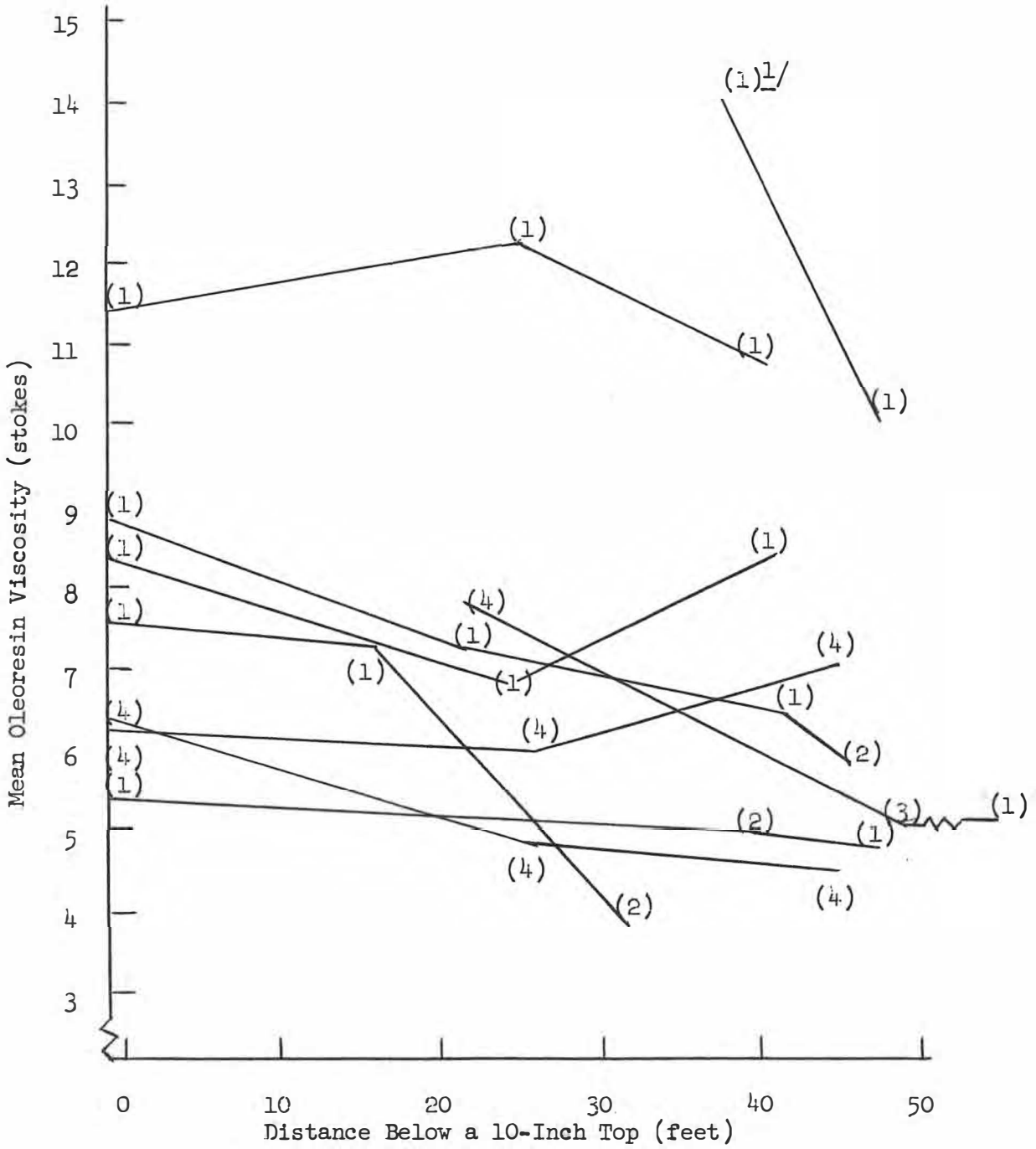
The Results

The viscosities for the ten oleoresin samples at the three temperatures are plotted on a log-log scale in figure 14. The resulting lines indicate a slightly curvilinear log-log relationshio rather than the straight-line relationship stated by Schopmeyer. All of the samples showed this curve regardless of whether they were of high, intermediate, or low viscosity. It is possible that the equation describing these lines is a polynomial. Furthermore, as previously noted by Schopmeyer, the slopes of samples with high and with low viscosities were different. This resulted in a convergence of the lines at higher temperatures. Hence, the equations for high and low viscosities would not be the same. Regardless of such mathematical complications, these curves facilitated the visual estimation of viscosities at 30°C. for samples whose viscosities had been determined in the field at temperatures of approximately 22°C.

Viscosity and Oleoresin Composition

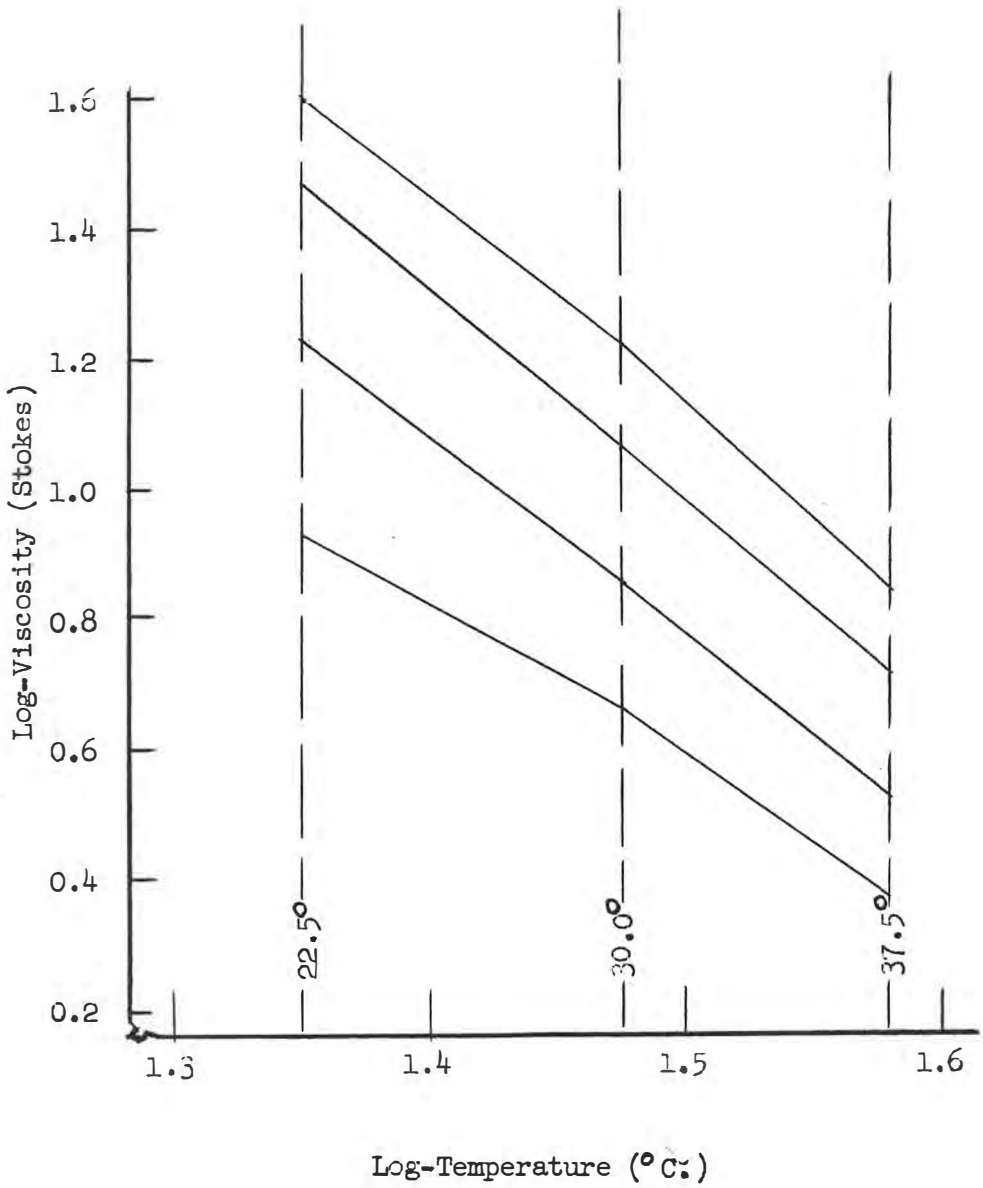
The preceding sections have discussed how oleoresin viscosity varies; it is the purpose of this section to consider why it varies. The publications by Smith and by Runckel and Knapp show the manner in which viscosity decreases with an increase in the amount of turpentine in the oleoresin. Mergen, Hoekstra and Echols (1955) write: "A high viscosity probably reflects a lower turpentine content of the oleoresin." Turpentine, the steam-volatile fraction of oleoresin, functions as an organic solvent for the resin acids comprising rosin. It is reasonable that the more solvent there is present the less viscous the solution should be. Similarly, changes in chemical composition of the solvent should alter its solvent action.

Figure 13. -- The viscosity of oleoresin obtained at various heights on the boles of nine trees.



1/ Number of samples at each height.

Figure 14. -- The viscosity of oleoresin at three temperatures.



Turpentine is composed of various combinations of aliphatic hydrocarbons, terpenes, and some sesquiterpenes and diterpenes. These substances vary in viscosity and solvent action; they all can be identified by their physical properties. Several workers have analyzed the turpentine from individual trees (Black and Thronson, 1934; Oudin, 1939, pp. 123-125; Scheuble, 1953). They all have found that individual trees vary considerably in the physical properties of their turpentine. Oudin and Scheuble both found that there does not seem to be any effect of season upon the physical constants.

From these facts one might expect that the viscosity of oleoresin would be almost completely determined by the composition of the turpentine and the amount of turpentine. The composition of the rosin might also affect viscosity. One method of computing potential viscosity might be to determine the specific gravity of oleoresin. Oleoresin specific gravity would give composite expression of the quantity of turpentine and chemical composition both of rosin and turpentine. C.S. Schopmeyer[16/], using this procedure, found a very good linear relationship between viscosity and oleoresin specific gravity. However, oleoresin specific gravity provides only an estimate of oleoresin composition, and its measurement is fraught with many difficulties. For this reason the decision was made to use the direct approach of correlating quantitative and qualitative changes in turpentine with variation in viscosity.

The Experiment

The materials for study were some of the oleoresin samples from which viscosity determinations had been made. These were the oleoresin samples collected from plots 1-3 during the 1953 field season. Analyses were made for the amount and composition of turpentine in each oleoresin sample. The oleoresin was steam distilled, and the turpentine was collected in a graduated volatile oil receiver. The yield of turpentine was measured gravimetrically to 0.01 grams and was expressed as a percent of the total amount of oleoresin. After the yields had been determined, each turpentine sample was sealed in a screw-top vial with a few crystals of anhydrous sodium sulfate. The samples then were refrigerated at 5°C. for at least 24 hours. The refractive index and specific gravity of each dried sample were measured. Finally, the data were subjected to correlation and regression analyses.

The Results

Several correlation analyses were made. The data used were from a series of 29 oleoresin samples. The highest correlations both between viscosity and the amount of turpentine in the oleoresin and between viscosity and the index of refraction of the turpentine were determined. Of the several linear, semi-logarithmic and log-log relationships tested, the highest correlations were between log-viscosity and percent of turpentine, $r_{yx} = -0.902$, and between log-viscosity and index of refraction of turpentine, $r_{yz} = -0.597$.

16/ C.S. Schopmeyer, Report of physiological studies made in 1950. Manuscript Report. Lake City Research Center, Southeast. Forest Experiment Station. 1950.

These two independent variables then were included in a multiple regression of the form: log Y = a + b X + c Z. The resulting regression equation was log Viscosity (in stokes) = 58.24 -0.0426 (% turpentine)-38.50 (N_d turpentine). The coefficient of multiple determination was $R^2 = 0.976$; the coefficient of multiple correlation was R = -0.988; and the standard error of the estimate was $SE_{logY.XZ} = 0.01683$. The coefficients of partial correlation all were highly significant: $r_{logYX.Z} = -0.982$, $r_{logYZ.X} = -0.937$, and $r_{XZ.logY} = -0.904$.

These values indicated that there was a very high correlation between variation in viscosity and variation in both of the independent variables. They also showed that viscosity of oleoresin was almost completely determined by the amount and composition of turpentine in the oleoresin. Thus, amount of turpentine must affect gum yield through its effects on viscosity. This is in agreement with the finding of Clark and Osborne (1948) for longleaf pine. Another interesting point is the highly significant partial correlation between yield of turpentine and the composition of the turpentine; the index of refraction of the turpentine decreases as the percent of turpentine increases. This is the first indication that turpentine composition changes with the amount of turpentine present in the oleoresin.

VARIATION IN THE NUMBER AND CAPACITY OF TRANSVERSE RESIN DUCTS

Further studies were undertaken to determine the variability in number and capacity of the transverse resin ducts. The earlier discussion of the applicability of Poiseulle's law to ponderosa pine oleoresin exudation provided some evidence that the rate of exudation was influenced both by the number and by the capacity of the transverse resin canals. A knowledge of the variability in these factors might be significant to an understanding of variation in the resistance of pines to bark-beetles. This variation was considered with respect to different positions on the bole and to rate of radial growth.

Variation with Respect to Position on the Bole

Here again on the basis of reduced oleoresin flow in the upper portions of the trees, one might expect to find fewer transverse resin ducts in that region. However, Hobert (1932) reports from his study of the basal 45 feet of young slash pines: "No consistent differences in the number of vertical (longitudinal) or horizontal (transverse) resin passages as related to height in the tree were found. . . ."

The Experiment

Wood specimens for a study of positional variation in transverse resin ducts were collected during the summer of 1952 at Blacks Mountain Experimental Forest. These wood blocks were taken from trees felled and bucked during logging. Four blocks were collected at each height along the bole, one each from the north, south, east and west aspects. The heights sampled were the stump, the upper end of the first 32-foot log, the lower end of the discarded top (50 to 70 feet above the stump), and ten feet below the tip (75 to 90 feet above the stump). At each sampling point blocks approximately one inch

square and containing as many as possible of the last fifty annual rings were cut out. Saw, axe, and chisel were used in the process. In some cases blocks could be obtained only from three of the four sides due to obstructions or due to the position in which the tree was lying. The blocks were marked with tree number, height, and aspect before they were placed in 50 percent ethyl alcohol. Records were kept of the distance between heights, the diameter at each height, the blocks obtained at each position, and the Keen class and risk rating of each tree.

In the laboratory the blocks were sectioned, and the resin ducts were counted and measured following the procedures described earlier. The data were grouped, and they were analyzed by statistical methods. The height means based on measurements at three or four aspects at each height were calculated for each of eight trees. These data for number and capacity of transverse resin ducts were subjected to variance analyses. Subsequently, the data were rearranged, and they were analyzed for variance due to aspect without regard to height. In this latter case the only data used were those in which each height had been sampled at all four aspects.

The Results

The results of all analyses of the variations in the number and capacity of transverse resin ducts at different heights on the bole are given in table 18. Table 19 presents similar information for different aspects. In general it appeared that change in aspect was not associated with variation in either the number or capacity of transverse resin ducts. In contrast, change in height was found to be highly significantly associated with changes both in the number and capacity of the transverse resin ducts. There were fewer ducts at mid-bole than either at the top or stump, and there was a general decrease in capacity from stump to tip. These changes are shown diagramatically in figure 15. Table 18 also shows a significant component of variance to be the variance between trees at each height. This variance may have resulted either from the differences in sampling from tree to tree or from the genetic differences between trees.

Variation with Respect to Rate of Radial Growth

Hobert, working with slash pine, found "no evidence that the width of the annual ring bears any relation to the number of linear and fusiform rays per unit area of tangential surface." The transverse resin ducts are found in these fusiform rays. From this finding by Hobert, one might reason that there would be no correlation between rate of growth and number of transverse resin ducts. However, Mergen and Echols (1955), who also worked with slash pine, showed that both the size and number of transverse ducts increased as average ring width increased from 0.1 to 0.3 inches.

The Experiment

Transverse wood sections were used in the determination of the mean annual rate of radial growth during the past ten years. These sections were taken from the wood blocks described in the preceding study. They were stained and mounted just as were the tangential sections. The width of each annual ring was determined by means of an eyepiece micrometer at a magnification of 60x. Three measurements were made of each annual ring. From these measurements the mean annual increment for the past ten years was computed.

Table 18.—Analyses of data pertaining to the variation in the number and capacity of transverse resin ducts at different heights on the bole

Source of variation	ANALYSES OF VARIANCE: Number of Ducts/mm² df	SS	MS	F	Capacity of Ducts $\overline{(ab)}^2$ df	SS	MS	F
Between heights	3	.09759	.03253	11.890***	3	.08571	.02857	7.151***
Within heights, between trees	7	.15959	.02280	8.333***	7	.08465	.01209	3.027*
Error	21	.05746	.00274		21	.08390	.00400	
Total	31	.31464			31	.25426		

t tests

Comparing 1/	Mean Number		t	Mean Capacity		t
(1) (2)	(1)	(2)	(df=14)	(1)	(2)	(df=14)
X and T	.4131	.4080	.108	.3120	.3540	1.080
X and M	.4131	.3521	1.377	.3120	.3794	1.942
X and B	.4131	.5060	2.249*	.3120	.4542	3.618**
T and M	.4080	.3521	1.200	.3540	.3794	0.663
T and B	.4080	.5060	2.243*	.3540	.4542	2.358*
M and B	.3521	.5060	4.137***	.3794	.4542	1.933

1/ X = 10 feet below tip; T = 10 inches diameter; M = top of first 32-foot log; B = stump.

* Variance or difference between means is significant at the .05 probability level.

** Variance or difference between means is significant at the .01 probability level.

***Variance or difference between means is significant at the .001 probability level.

Table 19.—Analyses of data pertaining to variation in the number and capacity of transverse resin ducts at different aspects on the bole

Source of Variation	ANALYSES OF VARIANCE: Number of Ducts/mm² df	SS	MS	F	Capacity of Ducts (ab)² df	SS	MS	F
Between 4 aspects	3	.01945	.00648	1.240	3	.01212	.00404	1.085
Within aspects between trees and heights	14	.61504	..043932	8.398***	12	.56882	.04740	12.729***
Error	42	.21970	.005231		36	.13408	.00372	
Total	59	.85419			51	.71502		

*** Variance due to difference between trees and positions is significant at the .001 probability level.

The data from 91 wood blocks pertaining to growth and to number and capacity of transverse resin ducts were subjected to regression and correlation analyses.

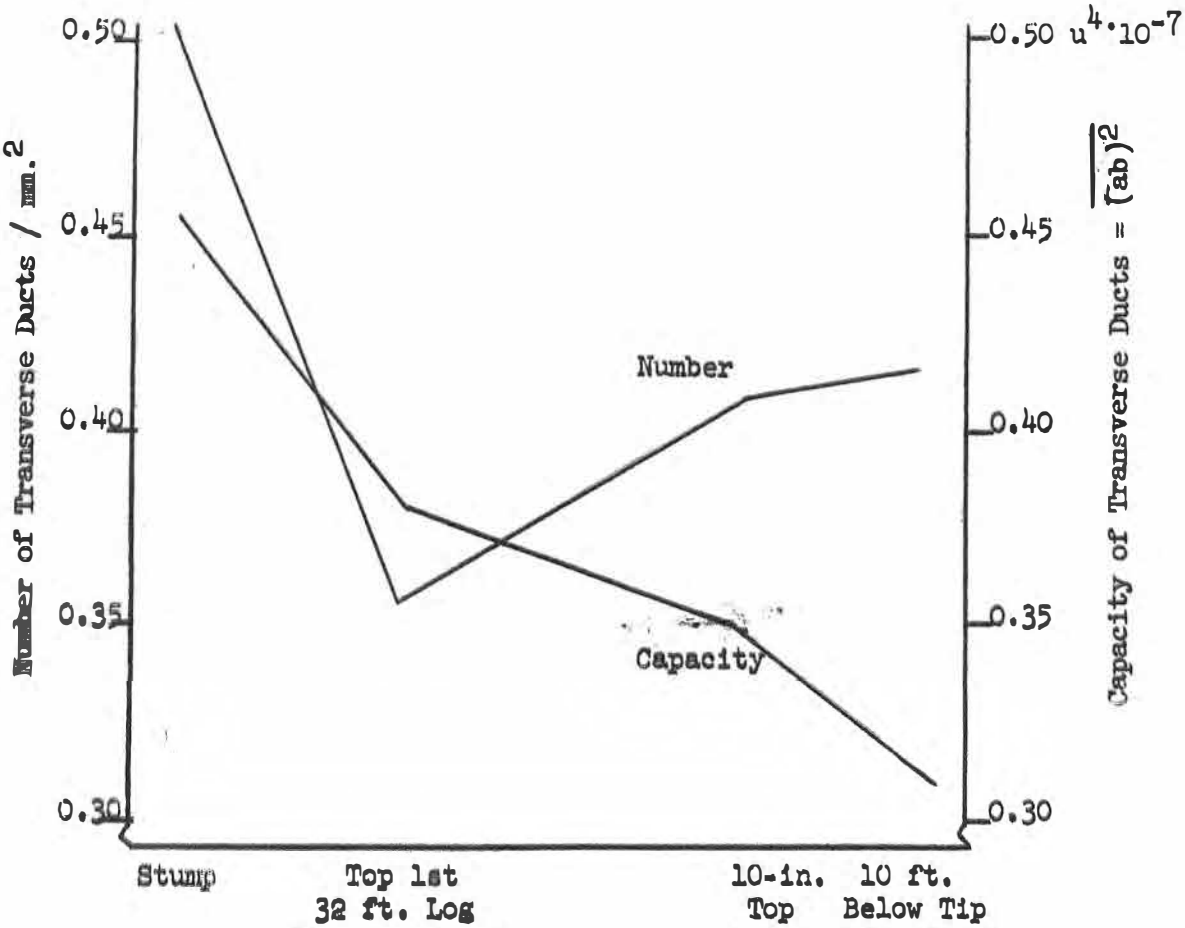
The Results

In the first analysis which was made it was determined that there was a highly significant negative correlation, $r = -0.386$, between the number of transverse resin ducts per mm^2 and the mean annual radial rate of growth during the period 1943 to 1952. This indicated that approximately 15 percent of the variation in number of resin ducts was inversely associated with variation in growth. The coefficient of regression of the number of ducts on growth was very highly significantly different from zero. These statistics indicated that variation in the number of transverse resin ducts was significantly associated with variation in the rate of growth; increases in number were associated with decreases in growth. This is in contradiction both to the prediction from Hobert's finding and to the finding of Mergen and Echols. This negative association of number with growth may be related to variations in the number of longitudinal resin ducts. This will be considered further in a later section.

The analysis of the correlation between the capacity of the transverse resin ducts and the mean annual growth gave no indication of a relation between capacity and growth. Neither the coefficient of correlation, $r = + 0.029$, nor the coefficient of regression of capacity on growth showed a significant deviation from the null hypothesis of no association between capacity and growth. This again did not agree with the results of Mergen and Echols.

Perhaps the differences in age of material, size of sample, rate of growth, and species in these studies were responsible for the discrepancies in results which were obtained.

Figure 15. -- The number and capacity of transverse resin ducts at different heights on the bole[1/].



1/ Points are means based on values derived from three or four samples at each height on eight trees.

Variation with Respect to the Vertical Resin Duct System

It has been recognized since the time of Mayr (1884) that the longitudinal and transverse resin ducts comprise an interconnected open system. Oleoresin is produced and moves through the stem via this system. There exists some controversy both as to the sequence of development and as to the stimuli responsible for the initiation of the morphogenetic processes by which the system is developed. Kirsch (1911) proposed that the stimulus results from excess concentrations of food material and that longitudinal ducts arise from transverse ducts. Thomson and Sifton (1925) presented the more plausible theory that the stimulus is associated with wounding, and they, like Mayr and others, were of the opinion that the transverse ducts develop from the longitudinal ducts. Regardless of the conflict in these concepts, it seems safe to follow the conclusion of all of these workers, that both the longitudinal and transverse elements of this system arise from the same stimuli. On this basis one might predict that the concentration of transverse elements would be related to the concentration of longitudinal elements.

The Experiment

This relationship between the transverse and longitudinal elements was investigated. The transverse wood sections discussed in connection with the preceding experiment provided the material for the study. The tangential length of the annual rings was determined to 0.1 mm. by means of the mechanical stage. Counts were made of the number of longitudinal resin ducts in each ring and in the outer 5 mm. of xylem. After simple computation, values were obtained for density of ducts per square millimeter of the transverse wood surface as well as for density of ducts per tangential centimeter of the last ten annual rings. The interrelation of longitudinal and transverse elements was determined through statistical analyses of data from 84 wood blocks.

The Results

From the analyses of the data it was determined that there existed a very highly significant correlation, $r = +0.312$, between the number of transverse resin ducts per mm^2 and the number of longitudinal resin ducts per tangential centimeter of the outer 5 mm. of the wood. That is, as the number of longitudinal elements increased, the number of transverse elements increased.

Other analyses showed that there was a very highly significant negative correlation, $r = -0.283$, between the density of transverse resin ducts and the density of longitudinal resin ducts in the outer ten annual rings.

From these analyses the prediction of a relationship between density of transverse resin ducts and density of longitudinal resin ducts was validated.

LONGITUDINAL RESIN DUCTS WITH RESPECT TO OLEORESIN EXUDATION

Most of the early workers, who engaged in research into the fundamental basis of turpentining, delved into the relationship between oleoresin exudation and the macroscopic longitudinal resin ducts. With respect to ponderosa pine it is important to note at this point that the transverse resin ducts of untapped xylem usually are devoid of oleoresin; the epithelial cells are completely distended, filling what would be the resin canal. Thus, the great mass of oleoresin exuding from a tapped wood surface must come through the transverse ducts from the connecting longitudinal resin ducts. These latter ducts then must serve in the capacity of an oleoresin reservoir. One might expect that oleoresin exudation would be correlated with variations in numbers of longitudinal resin ducts.

Density of Longitudinal Resin Ducts with Respect to Oleoresin Exudation

Previous work on the relation between yield and longitudinal resin ducts has been inconclusive. It is typified by this quotation from Ivanov:

> "The question of the number of resin ducts appears to be very important in the process of chipping although one must note right here that the number of resin ducts does not always serve as an indication of the ability of the tree to yield gum. Münch could not at all obtain any correlation between the number of resin ducts and gum yields. Trees with large yields frequently had less resin ducts than trees with lesser yields. In our laboratory, Miss Shaternikova has revealed that at times when the number of resin ducts increases the yields decrease. Evidently the number of resin ducts is far from being the dominating factor, the effect of which may be overshadowed by the activity of other factors. . . ."

Mazek-fialla (1948) in a more recent study confirms this opinion. He also was not able to show a correlation of yield with either the density of longitudinal resin ducts per square centimeter or the diameter of these ducts. On the other hand, Harm (1953) in his investigations of Pinus nigra found a significant correlation between the yield of oleoresin and the total cross-sectional area of the longitudinal resin canals in three year-old shoots.

Data pertaining to the relationship between density of longitudinal ducts and oleoresin exudation were available from various phases of this investigation. These have been presented here as a matter of record for ponderosa pine. Variations in density of longitudinal ducts also were considered with respect to rate of radial growth.

The Experiment

The data for study were collected in connection with the investigation of the applicability of Poiseulle's law to oleoresin exudation. For that study the 24-hour yield of oleoresin from each wound was determined as described on page 9 . Wood blocks were taken from these wounds, and transverse sections were prepared for study. On each section the length of the rings was measured, and the number of resin ducts in each annual ring and in the outer five mm. of xylem were counted. From these data computations were made of the density of resin ducts per tangential centimeter in the outer five mm. of sapwood and in the outer 5, 10, 15, and 20 annual rings. The regressions of yield on resin duct densities and the correlations between these variables were calculated.

The Results

Table 20 presents the results of the calculations. Oleoresin yield during the first 24 hours after tapping was significantly correlated with the density of longitudinal resin ducts only in the outer 20 annual rings. This finding is significant for it indicates an association in which approximately 28 percent of the variation in yield of oleoresin can be associated with positive variations in the oleoresin reservoir in the wood. Implications of this finding are rather difficult to assess. One conclusion might be that at least the resin ducts in the outer 20 annual rings contribute to oleoresin flow. For the slow-growing trees used in this study, twenty rings would amount to approximately the outer ten mm. of sapwood.

Density of Longitudinal Resin Ducts with Respect to Rate of Radial Growth

Many workers have been able to demonstrate a significant correlation between the concentration of ducts in the longitudinal resin system and the rate of radial growth. Münch, studying 80-130 year old trees, expressed this relationship algebraically as $d = 40 + 30/b$. In this equation d was the number of resin ducts per square centimeter of wood, and b was the width of the average annual ring in millimeters. This equation indicated that trees with slower growth had a greater density of longitudinal resin ducts. Conversely, Hobert found that wood with wider rings had a higher density of resin canals. He studied wood from slash pine trees 14 to 19 years of age. The discrepancies in the relative rates of growth and the ages and species of pines studied by these two men may contribute to the opposing results which they obtained.

The Experiment

Data pertaining to the mean annual rate of radial growth during the period 1943 through 1952 were taken from the experiments described on pages 71 and 72. These data were supplemented with the numbers of longitudinal resin ducts per tangential centimeter of the outer five mm. of wood and of the outer ten annual rings. The regressions of longitudinal resin duct densities on mean annual rate of radial growth and the correlations between these variables were computed. It should be noted that the trees from which the wood blocks were procured were slow growing mature or overmature individuals, probably more than 300 years of age.

The Results

The density of vertical ducts in the outer five mm. of the sapwood was found to be extremely highly correlated with growth during the last ten years, $r = -0.538$. Thus 29 percent of the variation in longitudinal resin duct density was associated inversely with variation in growth rate; increases in growth were associated with decreases in density of ducts. The coefficient for the regression of resin duct density on radial growth was highly significantly different from zero.

Similarly, the density of vertical ducts in the outer ten annual rings of the wood was found to be extremely highly correlated with mean width of these same ten rings. The coefficient of correlation was $r = + 0.853$; the coefficient of determination was $r^2 = 0.728$. This latter statistic indicated that approximately 73 percent of the increase in duct density in ten rings was associated with increase in width of the same rings. Again the coefficient of linear regression of duct density on growth rate was highly significantly different from zero.

These results lead to the conclusion that as rings increase in width there are associated increases in the number of longitudinal ducts in each ring and decreases in the density of these ducts per unit area of wood. Thus, the results agree with Münch's but not with Hobert's finding: perhaps this is due to the greater similarity in the age of Münch's trees to those considered in this study.

RADIAL GROWTH RATE WITH RESPECT TO OLEORESIN EXUDATION

The observation has been made repeatedly in connection with turpentining operations that faster-growing trees generally produce more oleoresin in the long run. C.S. Schopmeyer and P.R. Larson (1954) have reported that a little over 40 percent of the total variation in slash and longleaf pine gum yields is positively associated with the number of rings in the last radial inch. Mirov (1930) worked with mature and overmature ponderosa pine. He reports that the highest yields of oleoresin were obtained from trees which showed the best rate of growth, but he found a very low correlation between growth and yield. These particular studies utilized long-term yield records. Although such records were not available from the tapping carried out in these investigations, an analysis was made to determine whether the flow of oleoresin during the first day after tapping was correlated with the radial growth rate.

The Experiment

Data obtained in other phases of this investigation were brought to bear on this question. The data for the experiment described on page 78 were supplemented with measurements of the mean annual rates of radial growth during the last 5, 10, and 15 years. The regressions of yield on these rates of growth and the correlations between these variables were calculated.

The Results

Variations in yield during the first 24 hours after tapping could not be shown to be significantly associated with variations in the mean annual radial growth rate during the past 5, 10, or 15 years. The statistics from these analyses are presented in table 20.

Table 20.—Twenty-four hour oleoresin exudation with respect to density of longitudinal resin ducts and mean annual radial growth

	n	Mean Number Longitudinal Resin Ducts	Mean Yield in Grams First 24 Hours	r
/cm. of outer 5 mm.	78	30.1 ± 1.2	6.34 ± 0.58	+.183
/cm. of outer 5 rings	77	20.7 ± 1.1	6.46 ± 0.62	-.028
/cm. of outer 10 rings	50	29.4 ± 2.0	6.86 ± 0.85	+.089
/cm. of outer 15 rings	35	38.8 ± 3.4	7.71 ± 1.12	+.179
/cm. of outer 20 rings	19	42.9 ± 3.8	7.45 ± 1.66	+.529*
		Mean Annual Radial Growth		
1948-52	79	0.68 ± 0.04	6.51 ± 0.61	-.199
1943-52	51	0.55 ± 0.04	6.95 ± 0.84	-.137
1938-52	37	0.43 ± 0.04	7.82 ± 1.07	-.018

* Difference of the coefficient from zero is significant at the .05 probability level.

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